Land-Use Intensification in Grazing Systems: Plant Trait Responses and Feedbacks to Ecosystem Functioning and Resilience

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A thesis
submitted in partial fulfilment
of the requirements for the Degree
of
Doctor of Philosophy
in the University of Canterbury
by

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2011

To Ludovic and Sofia, the most significant results that emerged from this research.

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Abstract

Land-use change is the single most important global driver of changes in biodiversity. Such changes in biodiversity, in turn, are expected to influence the functioning of ecosystems and their resilience to environmental perturbations and disturbances. It is widely recognised that the use of functional traits and functional diversity is best for understanding the causes and functional consequences of changes in biodiversity, but conceptual development has outpaced empirical applications. This thesis explores these ideas in grazing systems, which are expected to undergo rapid intensification of fertiliser use and grazing pressure to meet the growing global demand for livestock products.

First, a flexible framework for measuring different facets of functional diversity is described, and a new multidimensional functional diversity index, called functional dispersion (FDis), is presented. Second, two vegetation sampling methods are compared with regard to their ability to detect changes in vegetation composition. Third, shifts in plant trait distributions following land-use changes are quantified and compared to null models, and a maximum entropy approach is used to quantify the direction and strength of selection on each trait. Fourth, it is shown that these shifts in trait distributions have cascading effects on primary production, litter decomposition, soil respiration, and ultimately soil carbon sequestration. Finally, data from 18 land-use intensity gradients are used to show that land-use intensification reduces functional redundancy and response diversity, two components of biodiversity that are thought to influence ecosystem resilience to future disturbances.

This study illustrates (i) the importance of considering species functional differences to understand how plant communities react to changes in soil resource availability and grazing pressure, and (ii) how such changes directly, indirectly, and interactively control ecosystem functioning, as well as (iii) increasing the vulnerability of ecosystems to future disturbances.

Acknowledgments

I am grateful to the many people who have contributed to this project. First, without the constant support and help of my wife, Priscilla Fortier, this thesis would either be much shorter (so you can blame her), or would have been submitted much later. Our two children, both born during this 3-year research project, brought much joy and also gave me extra motivation to finish this thesis quickly and get a real job.

I am most indebted to my co-supervisor Dr David Scott, first for setting up and maintaining for almost three decades the unique long-term experiment that formed the basis of my PhD research, for kindly sharing his house during field work, for his tremendous help in the field, and for the many stimulating discussions I have had with him over the years.

My main supervisor, Dr David A. Norton, has provided constant encouragement and support thoughout this project. I am grateful for the opportunities he gave me to improve my teaching skills and to take part in an international collaborative research project. My co-supervisor, Dr Jason M. Tylianakis, has not only been very helpful and supportive in my research project, but he also introduced me to other sub-disciplines of ecology that I was not familiar with; this led to fruitful collaborations between him and me.

For their help during field work, I want to thank the following people: first and foremost, my wife Priscilla, but also Dr David Scott, J. Morgenroth, A. Williams, G. Pilon, K. Bott, J. H. Lapointe, K. Pellerin, K. Rondeau, J. Rondeau, M. Farr, B. Noonan, R. Iles, and T. Hoyle. E. Razavy Toosi kindly agreed to perform the dissolved organic matter analyses. L. Kirk, A. Leckie, and N. Pink have provided logistical support.

Other than my supervisors, who have provided valuable feedback on all chapters, this thesis has also benefited from insightful comments from: N. J. Gotelli, N. G. Swenson, and S. Villéger (Chapter 2), D. D. Briske, M. J. Anderson, and two anonymous reviewers (Chapter 3), H. Lambers, N. Gross,

R. K. Didham, M. M. Mayfield, and J. A. Wells (Chapter 4), H. Lambers, B. Schmid, J. B. Grace, B. Shipley, N. Gross, and K. W. Dixon (Chapter 5), and V. Novotny, C. A. Kremen, and two anonymous reviewers (Chapter 6).

Finally, I want to acknowledge generous financial support from the University of Canterbury (UC International Doctoral Research Scholarship 2007–2010, Graham Whyte Forestry Prize 2009), the Fonds Québécois de Recherche sur la Nature et les Technologies (FQRNT Doctoral Scholarship 2007–2010), and Education New Zealand (NZIDRS Scholarship 2008–2010). The Miss E. L. Hellaby Indigenous Grassland Research Trust and the School of Forestry (University of Canterbury) funded this research. The ARC-NZ Vegetation Function Research Network provided funding for Chapter 6.

Chapter I

Introduction

1.1 Human Domination of the Biosphere

We live on a human-dominated planet where very few truly wild areas remain (Vitousek et al., 1997; Sanderson et al., 2002). While 14% of the terrestrial land surface is under some form of protection, a mere 1% is set aside as wilderness areas (IUCN, 2007). Humans appropriate about a quarter of the Earth's terrestrial net primary productivity, and in large regions of the world this is as high as 60–100% (Haberl et al., 2007). Some even suggest that since the 1980s, human demand for resources has exceeded the Earth's biological capacity (Wackernagel et al., 2002). The considerable size of our "share of the planetary pie" (Foley et al., 2007) is not surprising, considering that around 35% of the Earth's usable lands are used for agricultural purposes (Asner et al., 2004; Foley et al., 2005; Leff et al., 2004; Ramankutty et al., 2008). Of all land uses on Earth, managed grazing (i.e., pastures and rangelands) is the single most extensive use, accounting for a quarter of the ice-free land surface (Asner et al., 2004).

An obvious implication of these global land-use patterns is that conservation of biodiversity must be considered not only within protected areas, but also within an agricultural context (Perrings et al., 2006). While conservation priorities for future reserves must clearly be set (Myers et al., 2000), it is unlikely that solely focusing on establishing more reserves will be sufficient for conserving biodiversity (Folke et al., 1996; Folke, 2006), particularly in agricultural landscapes (Bengtsson et al., 2003). However, ecologists have historically worked largely outside of agricultural systems (Robertson, 2000), and so a paradigm shift towards studying the agricultural matrix itself is needed (Norton, 2000; Perrings et al., 2006; Vandermeer and Perfecto,

2007). If it is acknowledged that a vast proportion of the Earth's ecosystems are managed primarily to sustain the 6–7 billion people that inhabit it, then the key research goals must concern the inherent trade-offs among ecosystem functions and services in these managed systems (Tilman et al., 2002; DeFries et al., 2004; Foley et al., 2005; Robertson and Swinton, 2005; Bennett and Balvanera, 2007; Kareiva et al., 2007). Examples of such trade-offs include the interactions between intensifying production and the loss of native biodiversity (e.g., Green et al., 2005; Hendrickx et al., 2007; Moller et al., 2008; Dorrough and Scroggie, 2008), alterations of biogeochemical processes (Matson et al., 1997; Tilman et al., 2001), or decreases in ecosystem resilience to unexpected change (Foley et al., 2005; Fischer et al., 2006; Bennett and Balvanera, 2007; Kareiva et al., 2007; Fischer et al., 2008b). However, prior knowledge of the context-specific response of ecosystem properties in response to land-use change is required to assess trade-offs (DeFries et al., 2004), and this is currently an important research need (Carpenter et al., 2006).

As a step towards this goal, the work presented in this thesis focuses on a long-term (27-year) experiment (Scott, 1999) representing a realistic gradient of land-use intensification in grazing systems (Bouwman et al., 2005) to evaluate changes in plant biodiversity and associated feedbacks to ecosystem functioning and resilience. Central to this thesis is the idea that approaches based on functional traits (*sensu* Violle et al., 2007) may help us to better understand and predict changes in biodiversity in response to land-use change (Cingolani et al., 2005; Gross et al., 2007; Dorrough and Scroggie, 2008; Quétier et al., 2007b; McIntyre, 2008), as well as its potential feedbacks to ecosystem functions and services (Lavorel and Garnier, 2002; Garnier et al., 2004; Díaz et al., 2007a; Garnier et al., 2007; Quested et al., 2007; Luck et al., 2009; Suding et al., 2008; Webb et al., 2010) and ecosystem resilience to future environmental change (Walker et al., 1999; Hooper et al., 2002; Elmqvist et al., 2003; Folke et al., 2004). This Chapter provides an overview of these issues and presents the general approach taken in this thesis.

1.2 Land-Use Change in Grazing Systems

1.2.1 The Ecological Footprint of Grazing Systems

Understanding the trade-offs associated with different management strategies in grazing systems is essential because even though ranching and farming in general has greatly contributed to human well-being, the current magnitude of the global agricultural enterprise does not come without significant environmental costs (Matson et al., 1997; Tilman et al., 2001). The fact that managed grazing typically occurs on marginal lands that are either too infertile (tropical regions), too dry (arid and semiarid regions) or too cold (mountain regions) for crop production leads to a particular set of syndromes (Asner et al., 2004), namely desertification of drylands (Millennium Ecosystem Assessment, 2005a), woody encroachment of semiarid grasslands (Archer et al., 1995), and tropical deforestation (Nepstad et al., 1999; Laurance et al., 2004). These ecosystem-level changes in turn lead to global environmental impacts such as increases in greenhouse gas emissions (Kaiser, 1997; Hartley and Schlesinger, 2000; Jackson et al., 2002) and alteration of global water vapour flows (Gordon et al., 2005). In addition, livestock are also major producers of greenhouse gases through excreta (Yamulki et al., 1998; Johnson et al., 2000). Other environmental impacts are felt at more regional scales, for example when overgrazing leads to soil erosion and degradation, which in turn alters the quantity and quality of downstream water flow (Le Maitre et al., 2007). Quantification of the trade-offs associated with different land-use choices can better guide policy and management (DeFries et al., 2004; Foley et al., 2005), yet our current understanding of ecosystem response to land-use changes in grazing systems is diffuse and fragmentary because of insufficient research (Asner et al., 2004).

1.2.2 Land-Use Intensification in Grazing Systems: An Unavoidable Reality?

The forecasted doubling in global food demand by 2050 (Alexandratos, 1999; Tilman et al., 2002), and increased demand for meat and other livestock products in developing countries in particular (FAO, 2005), is likely to in-

crease the pressure on grazing lands worldwide. Agricultural intensification and expansion are the main drivers of global biodiversity loss (Sala et al., 2000; Chapin et al., 2000; Pimm and Raven, 2000; Tilman et al., 2001; Foley et al., 2005), and some have argued that this may in turn jeopardise the provision of vital ecosystem functions and services, possibly even threatening human well-being (Millennium Ecosystem Assessment, 2005b; Díaz et al., 2006). Perhaps the best-known example of this is how the loss of bird or insect species in agricultural landscapes due to intensification negatively impacts ecosystem services such as pollination, pest control, and seed dispersal (Tscharntke et al., 2005; Kremen et al., 2002, 2007). If these concerns are justified, then a future challenge is to find ways to increase food supply while minimising agriculture-related biodiversity loss (Jackson et al., 2007a), or even restoring biodiversity in already degraded agricultural systems (Dobson et al., 1997).

Some have proposed that the best approach to minimise biodiversity loss in agricultural landscapes is by intensifying production on the best soils so as to spare land for conservation elsewhere (e.g., Waggoner, 1995), while others propose more extensive "wildlife-friendly" farming (e.g., Krebs et al., 1999; Vickery et al., 2004). There is still considerable debate over whether intensification or extensification should generally be less detrimental to biodiversity (Balmford et al., 2005; Green et al., 2005; Mattison and Norris, 2005; Vandermeer and Perfecto, 2005; Matson and Vitousek, 2006), or whether intensification actually leads to land sparing in the first place (Vandermeer and Perfecto, 2005; Ewers et al., 2009). However, beyond the fact that such a dichotomy may be overly simplistic (Jackson et al., 2007b; Fischer et al., 2008a), in the case of arid and semiarid grazing systems options may be too limited to justify such a debate. Indeed, extensifying grazing beyond their current extent in these regions would imply the unlikely scenario of converting croplands to rangelands (Asner et al., 2004). In the humid tropics, extensification of grazing means burning down more tropical forest for pasture conversion (Asner et al., 2004), which has dramatic and potentially irreversible impacts on biodiversity (Nepstad et al., 1999).

As a result, some degree of agricultural intensification in grazing systems at the global scale appears unavoidable in the near future, either by necessity

(in arid or semiarid regions) or perhaps as the lesser of two evils (in the tropics). The last three decades have seen large increases in livestock production, but these have been largely driven by the development of "landless" livestock production systems, where animals are kept primarily inside, relying to a large extent on food crops, roughage, and other feedstuffs (Naylor et al., 2005; Bouwman et al., 2005). However, it is predicted that the increased demand for livestock products in the next three decades will result in a ∼33% increase in global grass consumption in pastoral systems (which rely almost exclusively on grazing), and that this can only be achieved through greater fertiliser inputs (Bouwman et al., 2005). Such intensification raises concerns for biodiversity conservation, particularly in systems where grazing occurs in multi-species, semi-natural grasslands. The present thesis focuses on the potential functional consequences of changes in biodiversity in grazing systems under land-use intensification; this is explored in more detail in the following section.

1.3 Biodiversity and Ecosystem Functioning in Grazing Systems

1.3.1 Does Species Richness Matter to Ecosystem Functioning?

Ultimately, the functioning of an ecosystem is driven by the interaction of its individual biotic components with the abiotic environment (Chapin et al., 1997). Ecosystem functioning is a somewhat elusive term (Jax, 2005), and so it is defined here as "ecosystem properties" sensu Hooper et al. (2005): "the sizes of compartments (e.g., pools of materials such as carbon or organic matter) and the rates of processes (e.g., fluxes of materials and energy among compartments)". Positive relationships between biodiversity and ecosystem functioning found in high-profile experimental studies (e.g., Naeem et al., 1994; Naeem and Li, 1997; Tilman and Downing, 1994; Tilman, 1996; Hector et al., 1999; Tilman et al., 2006) have often been presented as a general justification for the case of biodiversity conservation, yet their interpretation and relevance to ecosystem management have been strongly criticised (Aarssen, 1997; Huston, 1997; Hodgson et al., 1998; Wardle et al., 1998; Huston et al., 2000; Lawler et al., 2002; Srivastava and Vellend, 2005). For instance, it has been argued that the random synthetic species assemblages used in these

studies do not represent well the changes in biodiversity that actually occur in the real world (Leps, 2004; Schläpfer et al., 2005; Srivastava and Vellend, 2005), and that the effects of diversity *per se* on ecosystem functioning in natural or semi-natural communities are weak relative to abiotic drivers (Huston and McBride, 2002; Kahmen et al., 2005; Grace et al., 2007) or human management (Schaffers, 2002). Moreover, most past biodiversity-ecosystem function research has largely focused on total plant aboveground productivity as a sole measure of ecosystem functioning (Hooper et al., 2005; Balvanera et al., 2006), yet it is important to focus on other important functions or services (Reiss et al., 2009), for example soil carbon sequestration (Jones and Alison, 2004).

While these experimental studies have led to much development on potential mechanistic linkages between biodiversity and ecosystem functioning (Loreau, 2000; Fridley, 2001; Kinzig et al., 2002), further realism needs to be integrated in future research for it to be of greater relevance for guiding management (Díaz et al., 2003; Srivastava and Vellend, 2005; Hillebrand and Matthiessen, 2009). In particular, there is a crucial need to explore how long-term changes to biodiversity brought on by changes in land use (e.g., land-use intensification in grazing systems) affect ecosystem functioning (Chapin et al., 2000; Mooney, 2002). Another critique of the relevance of past biodiversity-ecosystem function studies to conservation is that it is very unclear whether increased rates of ecosystem processes (e.g., primary productivity) are actually desirable in natural systems (Lawler et al., 2002; Srivastava and Vellend, 2005). On the other hand, high levels of functioning are clearly sought-after in managed agricultural systems (Vandermeer et al., 2002; Hooper et al., 2005), and it is no coincidence that the biodiversity-ecosystem function relationship forms the conceptual basis of agroforestry and intercropping systems (Trenbath, 1974; Vandermeer, 1989; Swift and Anderson, 1993).

Some attempts have been made to extrapolate results from experimental biodiversity-ecosystem function grassland studies to agriculture (Tilman et al., 1999; Minns et al., 2001), yet because the only form of management used in these studies has been fire (Tilman, 1996; Tilman et al., 2006) or mowing (Hector et al., 1999; Spehn et al., 2005) but not grazing, extrap-

olating their results to grazing systems should be done with great caution (Sanderson et al., 2004). Indeed, grazing herbivores directly influence plant composition and diversity (Milchunas and Lauenroth, 1993; Olff and Ritchie, 1998; Landsberg et al., 1999; Rook and Tallowin, 2003), and can also alter ecosystem properties either directly (e.g., increased nutrient cycling by free-ranging grazers in African savannas McNaughton et al., 1997) or indirectly through grazing-induced vegetation shifts (Pastor et al., 1988; Bardgett and Wardle, 2003; Bagchi and Ritchie, 2010). In addition, because most diversity-function studies have been relatively short-term experiments conducted in immature plant communities (Thompson et al., 2005), longer-term perspectives on the relationship between biodiversity and ecosystem functioning are needed (Symstad et al., 2003; Hooper et al., 2005); this is particularly relevant for grazing management, in which decisions typically involve large spatial and temporal scales.

Studies conducted in more intensive pasture systems (i.e., where plant biodiversity is "planned" by the farmer and where inputs are frequently used) reveal that plant diversity can increase forage productivity (Daly et al., 1996; Clark, 2001; Sanderson et al., 2005). Since the most widespread management approach is to sow only two species (i.e., a particular grass-legume mix) it has been recommended to use more species-rich mixtures for pasture establishment to increase the likelihood of matching appropriate species to particular site and climatic conditions (Sanderson et al., 2004). Still, increasing pasture or forage diversity has been found to have generally little effect on animal production or carrying capacity (Scott, 2001; Sanderson, 2005), although this little-studied relationship merits more attention (Sanderson et al., 2004).

In semi-natural grasslands and rangelands where plant biodiversity is not "planned", and where the primary form of management concerns the timing, intensity, and duration of grazing, the relationship between plant biodiversity and ecosystem functioning has been much less studied despite the global importance of this land-use type, which occupies vast areas of central Asia, sub-Saharan and southern Africa, south-eastern South America, south-western United States, Australia, and New Zealand (Asner et al., 2004; Foley et al., 2005). In such systems, the large spatial scales involved, as well as the high spatial heterogeneity of plant composition, environmental condi-

tions and grazing patterns can present obvious methodological challenges for assessing the links between grazing intensity, biodiversity, and ecosystem functioning.

1.3.2 The Response-Effect Functional Trait Framework

A promising approach to explore changes in biodiversity in response to land-use change, and their functional consequences, is to use a plant functional trait approach (Lavorel et al., 1997; Shugart, 1997; Lavorel and Garnier, 2002; Hooper et al., 2005; Díaz et al., 2007a). A trait-based approach allows regional or global comparisons of the effects of management on vegetation, despite taxonomic differences in plant composition. Such an approach has recently been used to explore global responses of vegetation in response to grazing (Díaz et al., 2007c). Moreover, empirical evidence suggests that of all components of biodiversity, it is functional diversity (i.e., the identity, abundance, and range of species traits; Tilman, 2001) that exerts the strongest control over ecosystem processes (Hooper and Vitousek, 1997; Díaz and Cabido, 2001; Naeem and Wright, 2003; Hooper et al., 2005) and associated ecosystem services (Díaz et al., 2006; Quétier et al., 2007a; Díaz et al., 2007a). Indeed, complementary resource use, one of the main proposed mechanisms underlying positive effects of biodiversity on ecosystem functioning (Loreau et al., 2001; Hooper et al., 2005), is best represented by quantifying how individuals (or species) within a community differ functionally from each other (Díaz and Cabido, 2001).

Scaling-up from plants to ecosystems (e.g., ecosystem-level functioning) requires knowledge on species composition and their relative abundance, as well as the functional attributes of these species (Violle et al., 2007; Suding et al., 2008). The "biomass ratio hypothesis" (Grime, 1998), which states that plant traits of dominant species weighted by their relative abundance determine ecosystem-level properties such as litter decomposition rates and net primary productivity (Lavorel and Garnier, 2002), has been supported in empirical studies conducted in European grasslands (Garnier and Laurent, 1994; Quested et al., 2007; Garnier et al., 2007; Quétier et al., 2007a; Vile et al., 2006; Fortunel et al., 2009). These studies illustrate the usefulness of

the functional approach for predicting ecosystem-level responses to different management strategies in rangelands. This approach has been formalised into the "response-effect" functional trait framework (Lavorel and Garnier, 2002; Hooper et al., 2002; Naeem and Wright, 2003; Suding et al., 2008), which stipulates that functional traits can help us to understand species' responses to environmental changes, and, in turn, how changes in community composition translate into changes in ecosystem functioning. Moreover, the response-effect framework can be extended to also consider measures of functional diversity, in order to assess potential complementarity effects (Díaz et al., 2007a).

Lack of plant trait data is a major hindrance to predicting ecosystem-level changes in land use, and so more standardised empirical studies (e.g., Garnier et al., 2007) are required. Such studies have promising applications given that knowledge of patterns of plant traits and ecosystem properties in response to different management strategies (i.e., grazing regime, fertilisation) is a critical first step to the development of state-and-transition conceptual models for the management of grazing systems (McIntyre and Lavorel, 2007), where the goal is to describe vegetation dynamics by a series of discrete "vegetation states" and the transitions between them (Westoby et al., 1989). In this thesis, the response-effect functional trait framework is used to evaluate biodiversity responses to land-use changes and associated feedbacks to ecosystem functioning.

1.4 Biodiversity and Ecosystem Resilience

In addition to the potential effects of biodiversity on ecosystem functioning, it has been suggested that biodiversity may provide "insurance" against unexpected environmental fluctuations (Yachi and Loreau, 1999). There is increasing awareness that many ecosystems exhibit sudden shifts between alternative stable states once critical environmental thresholds are passed (Scheffer et al., 2001), and rangelands were among the earliest examples of such non-linear dynamics (May, 1977). A generic example of such alternative stable states in rangelands are the desirable (from a production perspective) grassy vs undesirable woody states; each of these states can be

self-sustaining on a multi-decadal scale and the transitions between these can be rapid (Walker, 2002). This general non-equilibrium behaviour of rangelands (Gillson and Hoffman, 2007) has led to the development of non-linear models for rangeland management (Westoby et al., 1989; Cingolani et al., 2005).

Recognition of this non-equilibrium behaviour is important because although the concept of sustainable management is based on the constant, perpetual flow of ecosystem goods (e.g., food, timber, etc) from production systems, such an equilibrium-centred view may in fact lead to the exact opposite result. Indeed, managing production systems exclusively for sustained yield can lead to their eventual collapse (Holling, 1973). This "command-and-control" approach to natural resource management simplifies the system to a minimum, thereby reducing its resilience to unexpected changes (Holling and Meffe, 1996). Hence an alternative approach for the management of production systems lies in maintaining their resilience rather than controlling external factors to achieve short-term production stability (Gunderson and Pritchard, 2002; Folke et al., 2004). A management approach based on maintaining or enhancing ecological resilience acknowledges that ecosystem management is fraught with uncertainty and incomplete understanding, and consequently seeks to decrease the likelihood of ecological surprises that can arise from management errors or unexpected environmental change. Such a preventive approach appears particularly relevant considering the increased frequency of extreme-weather events (e.g., severe droughts) brought on by global climate change (Rosenzweig et al., 2007).

The concept of ecological resilience, which was first suggested by Holling (1973), is defined as the magnitude of disturbance a particular system can absorb before shifting to another state (Ludwig et al., 1997; Peterson et al., 1998; Gunderson, 2000). Such state shifts (e.g., grassland to shrubland) are characterised by changes in the function, structure, identity and feedbacks of a system, and are also often difficult to reverse or even irreversible (Folke et al., 2004; Walker et al., 2004). On more productive grazing lands (e.g., developed pastures), such sudden and unexpected state shifts may be reversed by the farmer through active management, because the higher productive potential of these lands will ensure that the economic returns obtained will

outweigh the costs of inputs (e.g., fertilisation, seeding). However, on less favourable lands where the only viable management strategy involves moving stock according to spatial and temporal resource fluctuations (McAllister et al., 2006), reversing such catastrophic shifts through management may not be economically feasible. Therefore, a preventive approach that maintains or enhances the resilience of desirable states in grazing systems is required. This preventive approach is useful to management insofar as it is defined a priori what the desirable states are, and what potential disturbances or environmental fluctuations are to be expected within a given system (Carpenter et al., 2001). For example, in most semi-arid rangelands, the desirable state (from a production perspective) is one dominated by palatable grasses, and disturbances can include (but are not restricted to) grazing, drought, and fire. Resilience in rangelands can be partly conferred through soil physical properties associated with water infiltration and storage (Tongway and Ludwig, 1997; Walker, 2002), but is also expected to depend on plant functional attributes (Landsberg, 1999; Walker et al., 1999).

With regard to the potential role of plant functional attributes in conferring ecosystem resilience, it is important to distinguish between response and effect traits (Lavorel et al., 1997; Landsberg, 1999), because plant traits that influence ecosystem properties may not necessarily be correlated with traits that influence how species respond to disturbance (Lavorel and Garnier, 2002). A hierarchical functional classification in which response groups are nested within particular effect groups (Hooper et al., 2002) may be useful to assess ecosystem resilience, and this approach is tightly linked to the earlier concept of ecological redundancy in ecosystems (Walker, 1992, 1995; Naeem, 1998). In that view, resilience critically depends on the functional response diversity within functional effect groups (Elmqvist et al., 2003; Folke et al., 2004). Within a community, a few dominant species may contribute to the bulk of ecosystem properties (i.e., ecosystem functioning) at a given time, yet less abundant species, which are functionally similar to dominant species but differ in their response to stress and disturbance, may provide "latent functionality" and thus maintain resilience of function through time (Yachi and Loreau, 1999; Walker et al., 1999; Hobbs et al., 2007).

Exploring how changes in management affect ecological resilience is pro-

mising, since it allows a type of "risk assessment" associated with different management scenarios. Given that agricultural intensification is likely to occur in grazing systems throughout the world because of the growing demand for meat products (Myers and Kent, 2003; Bouwman et al., 2005), one of the major challenges that humanity faces in the coming decades is how to increase productivity while ensuring that production systems stay resilient to unexpected change (Foley et al., 2005; Carpenter and Folke, 2006; Carpenter et al., 2006; Bennett and Balvanera, 2007). In this thesis, the hierarchical effect-response framework (Hooper et al., 2002) is used to assess potential effects of land-use intensification on functional redundancy and response diversity, and thus ecosystem resilience to future disturbances.

1.5 Thesis Outline

A necessary pre-requisite for measuring changes in functional diversity at the community level is the development of appropriate metrics and tools. As a step towards this goal, Chapter 2 reviews and extends current approaches for measuring functional diversity from multiple traits, and provides computational tools to implement the proposed extensions. In particular, a new functional diversity metric is presented, called functional dispersion (FDis), which is the multivariate analogue of the weighted mean absolute deviation. This metric is used in Chapter 4 to test for trait over- and under-dispersion, in Chapter 5 to test for functional diversity effects on ecosystem functioning, and in Chapter 4 as a measure of response diversity.

Measuring changes in plant biodiversity requires effective vegetation sampling techniques. In order to ascertain the efficacy of the technique used in this thesis, Chapter 3 compares two vegetation sampling methods in their ability to detect changes in vegetation composition following long-term experimental manipulations of soil resource availability and grazing intensity. The first method is a rapid visual ranking method, whereas the second one is more intensive percent cover method that uses several sub-quadrats.

Chapter 4 analyses plant responses to long-term manipulations of soil resource availability and grazing intensity, using a trait-based approach. Shifts in trait distributions are explored and compared to null models, and a max-

imum entropy approach is used to quantify the direction and strength of selection on each trait.

Chapter 5 is an application of the response-effect functional trait framework to understand how changes in plant functional traits following land-use changes in turn influence ecosystem functioning. By combining the strengths of long-term experimental controls with statistical controls (using structural equation modelling), it is shown that long-term manipulations of soil resource availability and grazing intensity cause shifts in plant functional composition and diversity, with cascading effects on primary production, litter decomposition, soil respiration, and soil carbon sequestration.

Chapter 6 uses data from 18 land-use intensity gradients from across the globe to show that land-use intensification generally reduces plant functional redundancy and response diversity, thus potentially reducing ecosystem resilience to future disturbances.

Finally, Chapter 7 summarises the findings from all chapters and highlights some directions for future research.

Chapter II

A Distance-Based Framework for Measuring Functional Diversity from Multiple Traits[1]

2.1 Summary

A new framework for measuring functional diversity from multiple traits has recently been proposed. This framework was mostly limited to quantitative traits without missing values and to situations in which there are more species than traits, although the authors had suggested a way to extend their framework to other trait types. The main purpose of this Chapter is to further develop this suggestion. A highly flexible distance-based framework to measure different facets of functional diversity in multidimensional trait space from any distance or dissimilarity measure, any number of traits, and from different trait types (i.e., quantitative, semi-quantitative and qualitative) is described. This new approach allows for missing trait values and the weighting of individual traits. A new multidimensional functional diversity index, called functional dispersion (FDis), is also presented; this index is closely related to Rao's quadratic entropy. FDis is the multivariate analogue of the weighted mean absolute deviation, in which the weights are species relative abundances. For unweighted presence-absence data, FDis can be used for a formal statistical test of differences in functional diversity. The `FD` R-language package is provided to easily implement this distance-based functional diversity framework.

[1] This Chapter has been published as:
Laliberté, E. and Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299–305.

2.2 Introduction

Functional diversity is thought to be a key driver of ecosystem processes (Hooper et al., 2005), ecosystem resilience to environmental change (Folke et al., 2004), and ecosystem services (Díaz et al., 2007a). This has led to the development of several indices for measuring functional diversity (e.g., Petchey and Gaston, 2002; Botta-Dukát, 2005). Recently, Villéger et al. (2008) have proposed three multidimensional functional diversity indices for continuous functional traits, each exploring a different aspect of functional diversity: functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv). Exploring different facets of functional diversity in multidimensional trait space, as they proposed, offers a meaningful framework for measuring functional diversity. That being said, their framework was mostly limited to quantitative traits without missing values and to situations where there are more species than traits, although they had suggested a way to extend their framework to other trait types. The main purpose of this Chapter is to further develop this suggestion, highlighting its strengths and pitfalls.

First, it is shown how the original framework of Villéger et al. (2008) can be generalised to a highly flexible distance-based framework to measure functional diversity from any distance or dissimilarity measure, any number of traits (including more traits than species), and from different types of traits (i.e., quantitative, semi-quantitative, and/or qualitative), while tolerating missing trait values and allowing the weighting of individual traits. This is a significant improvement over their original framework, which could only deal with quantitative traits, did not allow the use of only one trait or of more traits than species, did not tolerate missing trait values, and did not directly allow the weighting of individual traits.

A new and intuitive multidimensional functional diversity index is also proposed, called functional dispersion (FDis), that presents several desirable properties. FDis is the average distance in multidimensional trait space of individual species to the centroid of all species; it can account for species abundances by shifting the position of the centroid towards the more abundant species and weighting distances of individual species by their relative

abundances. FDis is the multivariate analogue of the weighted mean absolute deviation; this makes the new index unaffected by species richness by construction.

In order for this distance-based functional diversity framework to be easily implemented, the `FD` R-language package (cran.r-project.org/package=FD) was developed. It can compute the FRic, FEve and FDiv indices of Villéger et al. (2008) and the new FDis index under this framework, as well as three other functional diversity indices: the community-level weighted means of trait values (Lavorel et al., 2008), Rao's quadratic entropy (Rao, 1982; Botta-Dukát, 2005), and functional group richness based on a posteriori functional classifications (Petchey and Gaston, 2006). The flexibility of this distance-based functional diversity framework and its easy implementation in the `FD` package should greatly facilitate the measurement of functional diversity for a wide range of ecological applications.

2.3 A Flexible Distance-Based Framework

Villéger et al. (2008) suggested that ordination should be used when there are more traits than species (a situation that cannot be handled by their FRic and FDiv indices), or when qualitative traits are present. In particular, they proposed to use the principal coordinate analysis axes from a Gower dissimilarity matrix (Gower, 1971) among the species as the new traits to compute their functional diversity indices when there are qualitative traits in the original (species $\times$ trait) matrix. This is also useful when some traits are semi-quantitative, when missing trait values are present, and when individual traits need to be weighted differently, because the Gower dissimilarity index can handle all of these situations (Gower, 1971; Legendre and Legendre, 1998; Podani, 1999). That being said, Villéger et al. (2008) did not provide any details on how this approach should be implemented, but this is needed in order to better highlight its strengths and pitfalls. This is especially relevant given that the situations listed above (i.e., presence of qualitative and semi-quantitative traits, and/or missing values) are likely to be common in functional trait data sets. For example, about one-third of all plant functional traits from the standard list of Cornelissen et al. (2003) are

qualitative or semi-quantitative.

The original functional diversity framework of Villéger et al. (2008) can actually be generalised to a flexible distance-based functional diversity framework in which:

1. any appropriate distance measure of choice is computed from the (species $\times$ trait) matrix,

2. this distance matrix is analysed through principal coordinate analysis,

3. the resulting principal coordinates are used as the new traits to compute the functional diversity indices.

In that view, the original approach of Villéger et al. (2008) simply represents the particular case where all traits are quantitative and where the Euclidean distance is used. The distance-based framework presented here is in line with what they proposed: to use the (standardised) traits directly to compute functional diversity if all traits are quantitative, or to use the principal coordinates of a Gower dissimilarity matrix if some traits are qualitative (in the Gower dissimilarity, quantitative traits are ranged in the [0, 1] interval instead of being standardised). However, any distance measure can actually be used, not only the Euclidean distance or the Gower dissimilarity. Although one of these two measures (Euclidean and Gower) will be appropriate in many situations, other measures may be preferred for particular applications. For example, other dissimilarity measures can accommodate different types of variables and missing values (Estabrook and Rogers, 1966; Pavoine et al., 2009).

Such a distance-based framework is not new for the analysis of ecological data. For example, the use of principal coordinates as variables has already been presented in the context of multivariate analysis of variance (Legendre and Anderson, 1999) and general discriminant analysis (Anderson and Robinson, 2003). This previous work has pointed out an important issue that needs to be considered when using that approach, but which Villéger et al. (2008) have not mentioned: what should we do if principal coordinate analysis returns negative eigenvalues? Indeed, some distance matrices will

not allow the distance relationships among the objects to be fully represented in a Euclidean space (Gower, 1982). This problem can result from the use of a semimetric or nonmetric distance measure or from the presence of missing values (Legendre and Legendre, 1998); it can even arise with most of the metric distance measures (Gower, 1982). In all these cases, principal coordinate analysis can return negative eigenvalues. The corresponding principal coordinates are not real, and therefore cannot be used as traits to compute functional diversity. However, if one simply ignores these imaginary axes and uses only the ones with positive eigenvalues, not all the variation of the original trait data is represented, leading to biased estimates of functional diversity.

Three correction methods are available (Legendre and Legendre, 1998). The first two consist in adding the smallest possible constant to either the distances (Cailliez, 1983) or the squared distances (Gower and Legendre, 1986; Lingoes, 1971) so that all negative eigenvalues are eliminated. The third one, which does not work for all coefficients, consists of taking the square root of the distances (Legendre and Legendre, 1998, Table 7.2). More details on these corrections methods can be found in Legendre and Anderson (1999).

Another potential pitfall regarding the use of principal coordinates as traits concerns the standardisation of traits. Villéger et al. (2008) suggested standardising traits in order to make them dimensionally homogeneous and to put equal weight to each trait in the estimation of functional diversity. This is a sensible suggestion, given that we rarely know *a priori* if some traits are more important than others. As such, the R code that they provided to compute their functional diversity indices (www.ecolag.univ-montp2.fr/software) automatically standardises each trait, without allowing the user to choose otherwise. However, it is crucial that the principal coordinates are not standardised prior to the estimation of functional diversity. In a distance-based approach, if traits are to be standardised, this needs to be done prior to computing the (species $\times$ species) distance matrix. Principal coordinates are scaled to lengths equal to the square roots of their eigenvalues, or in other words to variances equal to the principal coordinate analysis eigenvalues divided by $(n-1)$: the first axis always represents the largest proportion of

variation, while the additional axes represent progressively smaller amounts of variation. Therefore, standardising the principal coordinates prior to the estimation of functional diversity would give equal weight to each principal coordinate, which in turn would distort trait space, leading to incorrect estimates of functional diversity. It would be unfair to blame Villéger et al. (2008) for this potential pitfall, as they never mentioned whether principal coordinates should be standardised or not when they are to be used as traits. However, their silence on the issue, coupled with the fact that their code automatically standardises traits before computing their functional diversity indices, could have led users to miscalculate functional diversity. The new `FD` package avoids this potential pitfall.

2.4 Weighting the Traits

Villéger et al. (2008) have suggested standardising all traits to mean 0 and unit variance to give the same weight to each trait in functional diversity estimation. As mentioned previously, this is justified by the fact that we rarely know *a priori* which traits are the most important. Nonetheless, weighting of individual traits can a useful tool for functional diversity estimation and has been identified as an important area for future functional diversity research (Petchey and Gaston, 2006). The Gower dissimilarity index can be programmed to provide different weightings to descriptors of mixed types, as suggested by Legendre and Legendre (1998). The `FD` package includes the `gowdis` function to compute the Gower dissimilarity coefficient, with options to assign different weights to individual descriptors and to treat semi-quantitative variables as described by Podani (1999). This coefficient is the default used in the `dbFD` function of the `FD` package to measure functional diversity under this distance-based framework when some traits are semi-quantitative and/or qualitative, or when weights are specified.

There is at least one obvious case where different weightings would be required for adequately estimating functional diversity. When, for a given qualitative trait (e.g., for flowering plants, pollinator type), an individual species can have more than one attribute (e.g., bees, flies, moths), this trait is typically reclassified into as many binary (0–1) variables as there are in-

dividual attributes for that trait (e.g., bee-pollinated, fly-pollinated, moth-pollinated). However, doing so artificially increases the weight given to that trait relative to other traits. A sensible solution is to give a weight $w_i = {}^{x_i}/_{b_i}$ to each binary variable required to reclassify the trait, where x_i is the original weight given to trait i, and b_i is the number of binary variables required to re-code trait i.

2.5 Functional Dispersion

One very intuitive measure of functional diversity for a community of s species on which t quantitative traits were measured is the dispersion (i.e., spread) of the s species in the t-dimensional space. In univariate statistics, dispersion can be estimated by measures such as the mean absolute deviation, the sum of squared deviations from the mean (SS), the variance, the standard deviation, or the range, among others. Villéger et al. (2008) proposed a valuable framework to explore distinct facets of functional diversity, but only their FRic index can estimate the dispersion of species in trait space. It does so through the volume of the minimum convex hull that includes all species, which itself is a multivariate analogue of the range. Although FRic is clearly useful, it is well known that the range is not a reliable estimator of dispersion because it is highly sensitive to outliers. In addition, FRic does not integrate information on relative abundances. Consequently, rare species with extreme trait values will greatly inflate FRic. This may or may not be a desirable property, depending on the application. On the other hand, the FEve and FDiv indices of Villéger et al. (2008) are interesting and can take into account the relative abundances of the species, but they do not estimate the dispersion of species in trait space. Indeed, they focus on the distribution of species within the convex hull independently of its actual volume (see Fig. 2.1). Hence the development of a reliable estimate of functional dispersion that could also consider species relative abundances would be useful.

Multivariate dispersion (Anderson et al., 2006) can be used as a multidimensional index of functional dispersion (FDis). In that view, FDis is the average distance of individual species to the centroid of all species in the community (Fig. 2.2a). Details on how to compute multivariate disper-

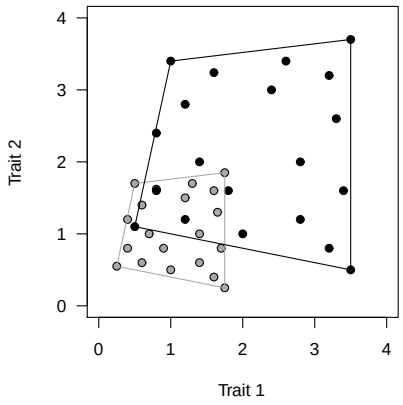

Figure 2.1: Two artificial communities C_1 (grey circles, grey polygon) and C_2 (black circles, black polygon) each composed of 20 species. Although the species in C_1 are obviously less dispersed in two-dimensional functional trait space than the species in C_2, both communities obtain a FDiv value of 0.808 and a FEve value of 0.935. In contrast the FDis values of C_1 and C_2 are 0.697 and 1.395, respectively.

sions in principal coordinate analysis space from any distance or dissimilarity measure and how to correct for negative eigenvalues are given by Anderson (2006). FDis can account for relative abundances by computing the weighted centroid of the $\mathbf{X} = [x_{ij}]$ (species $\times$ trait) matrix in the following way

$$\mathbf{c} = [c_{ij}] = \frac{\sum_{j=1}^{n} a_j x_{ij}}{\sum_{j=1}^{n} a_j}$$

where $\mathbf{c}$ is the weighted centroid in the i-dimensional space, a_j the abundance of species j, and x_{ij} the attribute of species j for trait i (Fig. 2.2b). This implies that x_{ij} is a quantitative trait, but Section 2.3 on page 16 describes how other trait types (i.e., semi-quantitative, qualitative) can be handled as well through principal coordinate analysis. FDis, the weighted average

distance to the weighted centroid $\mathbf{c}$, is then computed as

$$\text{FDis} = \frac{\sum_{j=1}^{n} a_j z_j}{\sum_{j=1}^{n} a_j}$$

where a_j is the abundance of species j and z_j is the distance of species j to the weighted centroid $\mathbf{c}$. These two modifications over Anderson's (2006) procedure essentially shift the position of the centroid towards the more abundant species and weigh distances of individual species to this weighted centroid by their relative abundances (Fig. 2.2b). When all species have equal abundances (i.e., presence-absence data, Fig. 2.2a), FDis is simply the unweighted average distance to the centroid as originally described by Anderson (2006). FDis has no upper limit and requires at least two species to be computed. For communities composed of only one species, FDis should be zero.

Simulations were run to compare FDis to the functional diversity indices of Villéger et al. (2008) and to Rao's quadratic entropy Q (Rao, 1982; Botta-Dukát, 2005; Ricotta, 2005), a popular multidimensional functional diversity index that is conceptually similar to FDis and can also account for species relative abundances. To do so, 20,000 artificial communities of 5 to 100 species drawn from a common pool of 500 species were created via the `simul.dbFD` function of the `FD` package. Values for three functional traits were generated following a normal distribution. Relative abundances were generated from a lognormal distribution. FDis was moderately positively related to FRic ($r = 0.425$, Fig. 2.3a) and FDiv ($r = 0.457$, Fig. 2.3b), and weakly with FEve ($r = 0.214$, Fig. 2.3c). On the other hand, FDis showed a strong positive linear relationship with Rao's Q ($r = 0.966$, Fig. 2.3d). Both FDis and Rao's Q were little influenced by species richness (FDis, $r = 0.274$, Fig. 2.3e; Rao's Q, $r = 0.264$, Fig. 2.3f). For completeness, simulations were repeated with presence-absence data (Fig. 2.4). Results were very similar, with the exception that FDiv and FEve were less associated with FDis ($r = 0.110$ and $r = 0.131$, respectively).

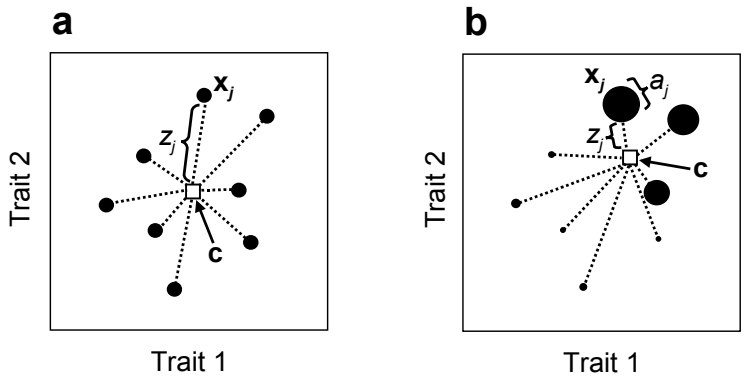

Figure 2.2: Example showing how functional dispersion (FDis) is computed. The n individual species in a two-dimensional trait space are represented by black circles whose sizes are proportional to their abundances. Vector $\mathbf{x}_j$ represents the position of species j, vector $\mathbf{c}$ is the centroid of the n species (white square), z_j is the distance of species j to centroid $\mathbf{c}$, and a_j is the abundance of species j. In (**a**), all species have equal abundances (i.e., presence-absence data). In that case, $\mathbf{c} = [c_i]$, where c_i is the mean value of trait i, and FDis is the mean of distances z of individual species to $\mathbf{c}$. In (**b**), species have different abundances. In that case, the position of $\mathbf{c}$ is weighted by the species relative abundances, such that it shifts towards the more abundant species. Individual distances z of species to $\mathbf{c}$ are weighted by their relative abundances to compute FDis.

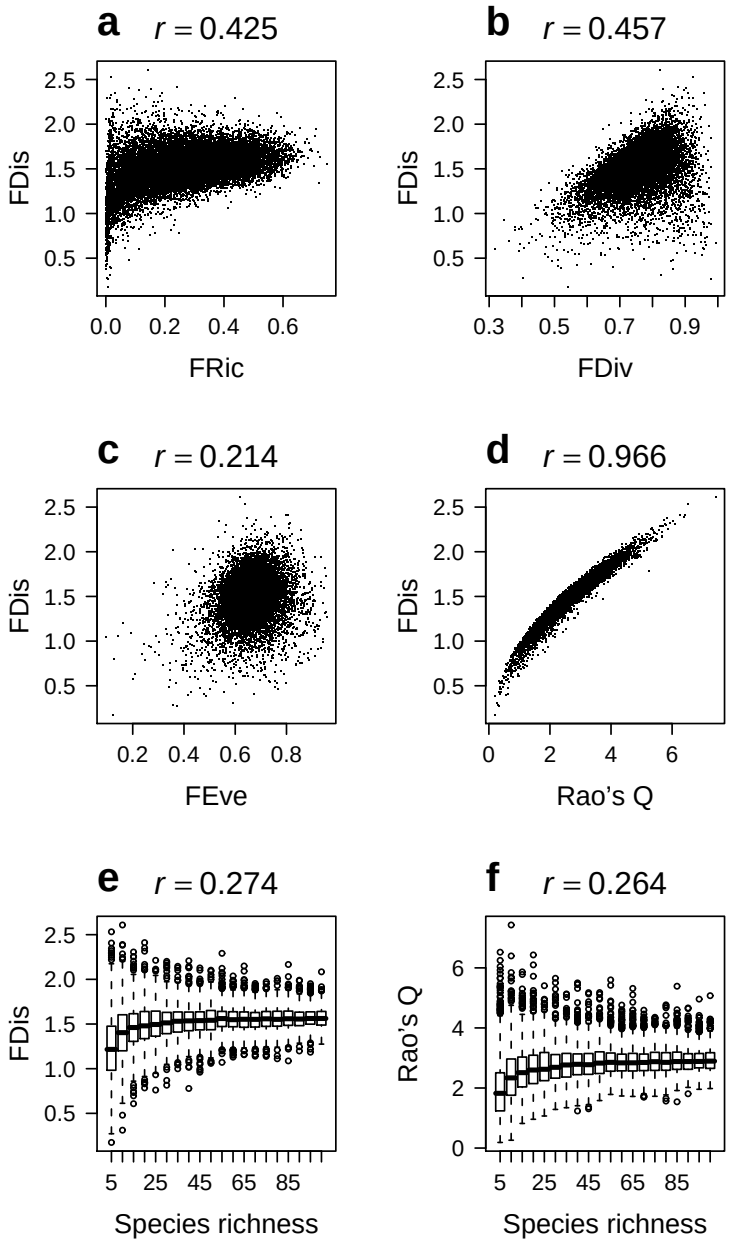

Figure 2.3: Simulation results (20,000 communities, abundance data). (**a**) Relationship between FRic and FDis, (**b**) FDiv and FDis, (**c**) FEve and FDis, (**d**) Rao's Q and FDis, (**e**) species richness and FDis, and (**f**) species richness and Rao's Q.

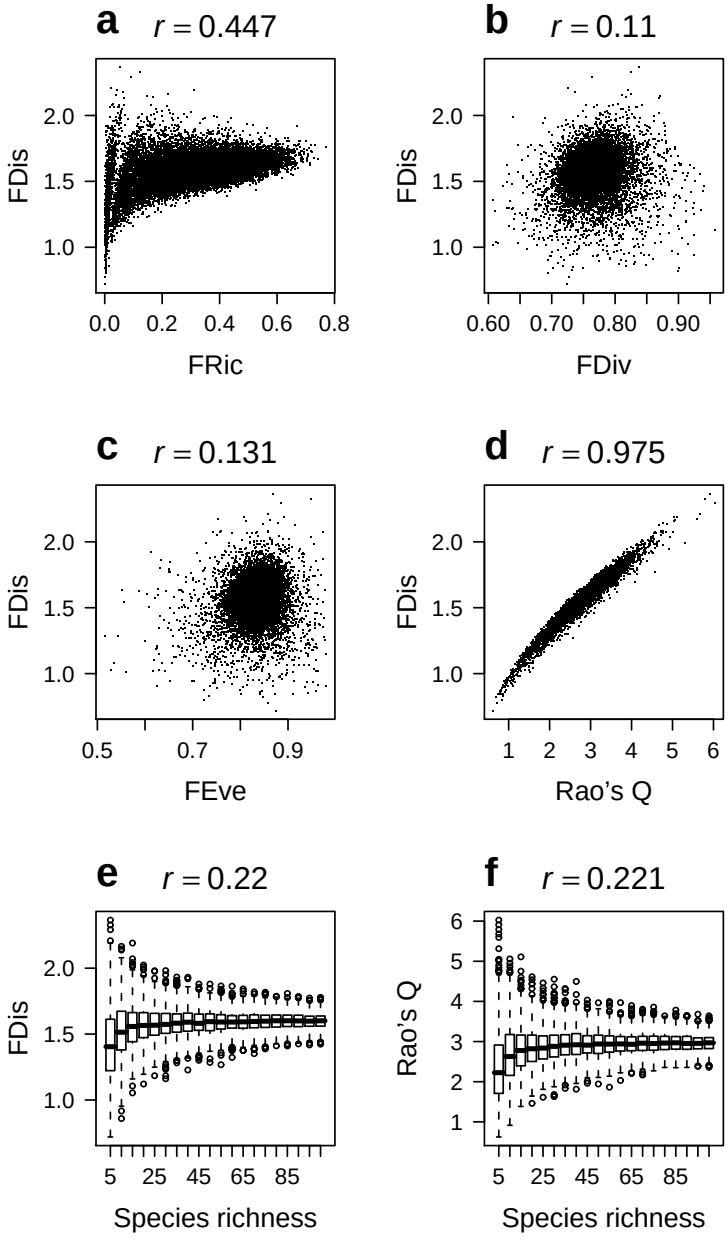

Figure 2.4: Simulation results (20,000 communities; presence-absence data). (**a**) the relationship between FRic and FDis, (**b**) FDiv and FDis, (**c**) FEve and FDis, (**d**) Rao's Q and FDis, (**e**) species richness and FDis, and (**f**) species richness and Rao's Q.

The strong positive correlation between FDis and Rao's Q was expected given that both indices aim at estimating the dispersion of species in trait space, weighted by their relative abundances. However, they do so differently. When abundances are frequencies (i.e., counts of individuals), Rao's Q expresses the mean distance between two randomly selected individuals (Botta-Dukát, 2005); Rao's Q is the multivariate analogue of the weighted variance. On the other hand, FDis is the weighted average distance of individual species to their weighted centroid, where weights are their relative abundances (Fig. 2.2); this is the multivariate analogue of the weighted mean absolute deviation. Although both indices are clearly associated, one potential advantage of FDis over Rao's Q is that in the unweighted case (i.e., with presence-absence data), it opens possibilities for formal statistical tests for differences in functional diversity between two or more communities through a distance-based test for homogeneity of multivariate dispersions (Anderson, 2006), which itself is a multivariate extension of Levene's (1960) test on absolute deviations. Moreover, because the mean absolute deviation is less sensitive to outliers than the variance, FDis should be less sensitive to species with extreme values than Rao's Q.

FDis is by construction unaffected by species richness, can be computed from any distance or dissimilarity measure (Anderson et al., 2006), can handle any number and type of traits (including more traits than species), is not strongly influenced by outliers, and can take into account species relative abundances. FDis also satisfies all criteria but the first one (i.e., to be constrained between 0 and 1 for convenience) of Mason et al. (2003) if traits are standardised prior to its computation. FDis does not satisfy the set monotonicity criterion (i.e., a subset of a community should be no more diverse than the whole community) of Ricotta (2005) because removing species that are close to the centroid effectively increases the average dispersion of species in trait space. This represents an interesting ecological signal, not a methodological artefact. In simulations (Fig. 2.3), satisfied the set concavity criterion of Ricotta (2005), since the total γ-diversity of the pooled set of communities was greater ($\text{FDis}_{\gamma} = 1.584$) than the average α-diversity of all communities ($\text{FDis}_{\overline{\alpha}} = 1.519$). Further investigation is required to confirm whether this property can be generalised.

2.6 Bridging the Gap Between Theory and Practice

For a functional diversity framework to be most useful, it has to be easily implemented by ecologists, if possible with freely available software. As such, the efforts made by Villéger et al. (2008) to provide the code to compute their functional diversity indices in the freely available R environment (R Development Core Team, 2010) is laudable. Likewise, the `FD` R package is provided to easily implement the distance-based functional diversity framework presented here. The `FD` package includes numerous elements of flexibility (Table 2.1). First, whereas the `F_RED` function of Villéger et al. (2008) only allowed quantitative traits to be used, the `dbFD` function of the `FD` package allows for a wide range of input options, including the use of a (species $\times$ species) distance matrix. Second, `F_RED` did not allow the use of more traits than species for any of the three functional diversity indices it returned. For FRic and FDiv, this was supported by the fact that no convex hull can be computed when there are more dimensions (i.e., traits) than points (i.e., species), but this was unnecessary for FEve, which does not have that limitation. The `dbFD` function can deal with any number of traits. Indeed, more traits than species can always be used for FDis and FEve. For FRic and FDiv, when the goal is to compare several communities, this problem is solved by selecting a subset of principal coordinates such that $t = s_{min} - 1$, where s_{min} is the number of species in the community with the fewest species and t the number of principal coordinates to be used as traits. However, doing so entails dimensionality reduction, which implies some loss of information. Such information loss can be quantified via the R^2-like ratio in principal coordinate analysis (Legendre and Legendre, 1998). Third, in `dbFD`, FRic is generally measured as the convex hull volume, but when there is only one quantitative trait it is measured as the range. For a single semi-quantitative trait, FRic is the range of the ranks. Conversely, when only qualitative and semi-quantitative traits are present, FRic is measured as the number of unique trait value combinations in a community.

Other multidimensional functional diversity indices were added in the `FD` package. The community-weighted means of trait values is a direct extension of the "biomass ratio hypothesis" (Grime, 1998) and represents functional

Characteristics	F_RED	dbFD
Input - traits		
Allows quantitative (i.e., continuous) traits?	✓	✓
Allows qualitative (i.e., categorical or nominal) traits?		✓
Allows semi-quantitative (i.e., ordinal) traits?		✓
Can have more traits than species?		✓
Can be a species × species distance matrix?		✓
Allows weighting of individual traits?		✓
Input - abundances		
Allows sites with only one species?		✓
Allows sites with only two species?		✓
Can be missing?		✓
Options		
Can standardise traits or not?		✓
Can weigh indices by abundances or not?		✓
Different ways of measuring FRic depending on the situation?		✓
Can FRic be standardised by the global hull volume (or other)?		✓
Can respect $s > 2^t$ condition when FRic is the convex hull volume?		✓
Computes Rao's quadratic entropy Q?		✓
Computes FDis (functional dispersion)?		✓
Computes community-weighted trait means?		✓
Computes *a posteriori* functional group richness?		✓

Table 2.1: Main differences between F_RED and dbFD.

composition (sometimes called functional identity). Because functional composition has been shown to be a key driver of ecosystem processes (e.g., Mokany et al., 2008), the inclusion of community-weighted trait means was important. Community-weighted trait means can be multidimensional, as it is a vector containing as many elements as there are traits. When the goal is to compare several communities, principal coordinates could be computed from the community-weighted trait means data, using an appropriate distance measure, and these axes could be used as an index of functional composition. As previously mentioned, correction for negative eigenvalues may be necessary. Multivariate analyses could then be used to compare functional composition between groups of communities (e.g., Legendre and Anderson, 1999) or to carry out spatial analysis of functional diversity (Legendre et al., 2005). Community-weighted trait means are generally used for quantitative traits, but the `FD` package extends it to qualitative and semi-quantitative traits. Another addition is functional group richness, which is computed from an *a posteriori* classification of species based on their functional traits (i.e., the data-defined approach of Gitay and Noble, 1997). This differs from commonly-used a priori classifications such as C_4 grasses, C_3 grasses, or legumes (e.g., Tilman et al., 1997), which generally follow a deductive approach (Gitay and Noble, 1997). Functional group richness computed from *a priori* functional classifications has been shown to be a poor predictor of ecosystem processes (Wright et al., 2006; Mokany et al., 2008), yet it is unclear whether this also applies to *a posteriori* classifications. It may turn out to be so, in which case functional group richness could still be useful for descriptive purposes.

2.7 Conclusions

Villéger et al. (2008) have set the stage well for the development of a multidimensional and multifaceted framework for functional ecology. The purpose of this Chapter was to improve their framework. First, it was described how the approach of Villéger et al. (2008) could be generalised to a flexible distance-based functional diversity framework. Second, a new functional diversity index was presented, functional dispersion (FDis). FDis is the weighted average

distance in multidimensional trait space of individual species to the weighted centroid of all species, where weights correspond to the relative abundances of the species. Finally, the `FD` R-language package is provided to easily implement the distance-based functional diversity framework. This distance-based functional diversity framework and its associated code represent significant improvements over the original approach described by Villéger et al. (2008), yet it is simply a second step and may certainly be improved upon in the future. Suggestions will be welcomed to make this distance-based functional diversity framework, and its implementation in the `FD` package, even more useful and flexible. Doing so will help in increasing the ability of ecologists to understand and predict the functional consequences of human-induced changes in biodiversity, a major contemporary goal for ecology.

Chapter III

Comparison of Two Sampling Methods for Quantifying Changes in Vegetation Composition under Rangeland Development[1]

3.1 Summary

Rapid vegetation sampling methods based on visual estimation are useful for monitoring changes in rangeland vegetation composition because large spatial and temporal scales are often involved and limited sampling resources available. In this Chapter, two sampling methods are compared in their ability to detect changes in vegetation composition following rangeland development: (i) species percent cover estimates within subplots (the percent cover method), and (ii) rankings of relative biomass of the ten most abundant species across the whole plot and the ratio of two of them (the visual ranking method). Both methods were applied on 30 experimental plots at year 26 of a long-term factorial trial of five soil fertility levels and three sheep grazing intensities. Multivariate statistical methods showed significant effects of experimental treatments (fertiliser level and sheep grazing intensity) and of vegetation sampling method (visual ranking vs percent cover) on vegetation composition. Importantly, no significant interactions involving sampling method were detected, indicating that the effect of sampling method was consistent across experimental treatments. Effects of fertiliser on vegetation composition were an order-of-magnitude greater than the effect of sampling method, while the latter was twice as important as the

[1] This Chapter is currently in press:
Laliberté, E., Norton, D. A., Tylianakis, J. M. and Scott, D. (in press). Comparison of two sampling methods for quantifying changes in vegetation composition under rangeland development. *Rangeland Ecology & Management*.

effect of grazing. Results were robust to differential weights given to relative abundances vs compositional changes. Differences between methods were primarily driven by the percent cover method giving lower abundance estimates of one relatively abundant species, lupin (a hybrid of *Lupinus polyphyllus* Lindl.), relative to the visual ranking method. These results support the use of the visual ranking method as a rapid yet powerful method for monitoring changes in vegetation composition under rangeland development.

3.2 Introduction

A wide array of different vegetation sampling methods are available for quantifying species abundance in plant communities (Müeller-Dombois and Ellenberg, 2003). Methods are generally judged on precision (how well does the sample represent the "true" value), repeatability among different observers, and efficiency (the amount of resources spent, particularly time, per unit information gained) (Symstad et al., 2008). With regard to long-term rangeland monitoring, efficiency is often a primary practical concern because of the large spatial and temporal scales involved, and the often-limited funding available (Stohlgren et al., 1998). As a result, rapid and cost-effective methods for monitoring rangeland vegetation have been proposed (e.g., Friedel and Chewings, 1988; Meentemeyer and Moody, 2000).

The listing or ranking of species in their descending order of abundance is commonly used in describing vegetation composition in a sample unit, and has been formalised in some sampling methods. In the dry-weight-rank technique ('t Mannetje and Haydock, 1963), this is done by visually ranking the first three most abundant species in subplot samples and assuming these are generally in fixed proportions of biomass, based on extensive earlier clip quadrat studies. The present work used visual ranking of up to ten species in a sample unit for their contribution to standing biomass (Scott, 1989), hereafter referred to as the "visual ranking" method. Compared to the dry-weight-rank technique, the visual ranking method shifts the assumption from the constancy of the species proportions to a log-linear relationship whose gradient can be determined by estimating the abundance ratio between two species (generally between the fifth- and first-ranked species; Scott, 1989).

The rationale behind such visual ranking methods is that much information on a given plant community can be obtained by simply knowing the relative order of importance for the first few dominant species ('t Mannetje and Haydock, 1963; Scott, 1989). The visual ranking method has since been used in different applications (Linklater and Cameron, 2000; Scott, 2001, 2007; Linklater and Cameron, 2009). This method was shown to be little influenced by observer (Scott, 1989), but has not yet been compared to other vegetation sampling methods.

The objective of the present study was to compare the visual ranking method with a more field-intensive vegetation sampling approach using several randomly-located sub-quadrats per plot, from which percent cover of all vascular plant species was assessed visually (hereafter referred to as the percent cover method, or PC; Müeller-Dombois and Ellenberg, 2003). However, since the visual ranking method only estimates the ranks of the most abundant species in a sample unit, the objective was not to compare the ability of each method to detect rare species, as other authors have previously done in comparisons of other sampling methods (West and Reese, 1991; Stohlgren et al., 1998; Prosser et al., 2003; Symstad et al., 2008; Godínez-Alvarez et al., 2009). Instead, the objective was to compare the relative ability of the visual ranking and percent cover methods to detect changes in vegetation composition following contrasting rangeland development strategies (fertilisation, irrigation, and grazing intensity). Vegetation composition is defined here as the relative abundances (i.e., which species are present, and in what proportion) of the most abundant plant species within a given community. If the differences in vegetation composition identified by the visual ranking and percent cover methods are consistent across development treatments, then either method could be used for monitoring in this type of situations. Conversely, if the methods differ in their ability to discriminate compositional changes caused by treatments (i.e., if there is a significant treatment $\times$ method interaction), then the more sensitive sampling method may be preferred.

3.3 Materials and Methods

3.3.1 Study Area and Site

The study was conducted on the AgResearch trial site at Mount John (Fig. 3.1), west of Lake Tekapo in the Mackenzie Basin of New Zealand's South Island (43°59'S, 170°27'E, 820 m above sea-level). The climate is semi-continental with an average of 1772 degree-days above 5 °C and a mean annual temperature of 8.7 °C, with a mean monthly maximum of 14.9 °C in January (warmest) and mean monthly minimum of 1.7 °C in July (coldest). Mean annual rainfall is 601 mm and is uniformly distributed throughout the year. The average annual moisture deficit is 445 mm. Prevailing winds are from the north-west and are often strong. Soils are Humose, Orthic Brown (Hewitt, 1998), between 45 to 90 cm deep, and were developed from greywacke and argillite rock till material subsequent to the retreat of the Tekapo glacier about 13 000 years ago. The dominant vegetation type prior to human settlement in the area is likely to have been short-tussock grassland with a variable woody component, probably near the tall tussock (*Chionochloa* sp.)/short tussock (*Festuca novae-zelandiae* Hack. Cockayne) transition (McGlone, 2001). Early human occupation started around 700–800 years ago, and has been linked with increased fire frequency (McGlone, 2001). Extensive grazing by sheep began in the area in the 1850–60s and remains the most important land-use today.

3.3.2 Experimental Design

The experiment is described in detail by Scott (1999) and is only summarised here. In 1982, a homogeneous mixture of 25 agricultural grass and legume pasture species (Table 3.1) was sown using a rotary hoe drill within a 3-ha area of depleted fescue tussock (*F. novae-zelandiae*) grassland dominated by the exotic mouse-ear hawkweed (*Hieracium pilosella* L.) and an estimated 30–40 other vascular plant species. This vegetation type is representative of large areas of New Zealand rangelands (Wardle, 1991). The trial followed a split-plot design consisting of two spatial replications (blocks), each split into five whole plots receiving one of the following five nominal fertiliser

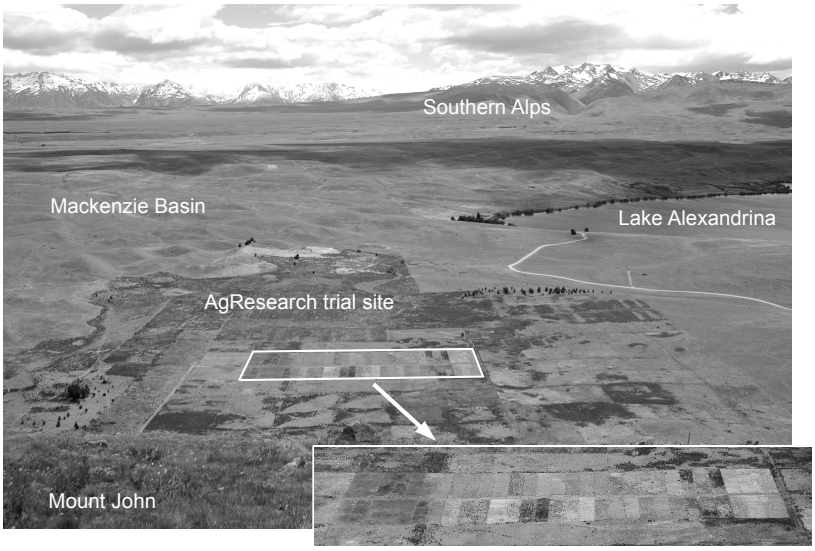

Figure 3.1: Aerial view of the study area and AgResearch trial site at Mount John, located in the Mackenzie Basin of the South Island of New Zealand. The white rectangle shows the location of the experiment used in the present study (inset: close-up view of the 8×50-m experimental plots).

treatments: 0, 50, 100, 250, and 500 kg ha^{-1} yr^{-1} of sulphur fortified superphosphate (i.e., a P/S fertiliser), which is typical of Australian and New Zealand legume-based developed pasture systems. The whole plots receiving 500 kg ha^{-1} yr^{-1} were also irrigated fortnightly from November to May of each year. Fertiliser was applied each year for the first 20 years of the experiment. The fertiliser was applied annually to plots in early spring. Annual variations in the analysis of P and S content of the superphosphate were considered. The actual mean P and S rates applied over the first 10 years of the experiment, in terms of applied P+S, were: $0 + 0$, $4.1 + 17.6$, $8.9 + 26.0$, $22.7 + 54.5$, and $46.8 + 114.8$ kg ha^{-1} yr^{-1} for the 0, 50, 100, 250 and 500 kg ha^{-1} yr^{-1} treatments, respectively (Scott, 1999).

Each whole plot was further split into six 8×50-m subplots (hereafter simply referred to as "plots") corresponding to a two-way factorial design involving sheep grazing intensity (lax, moderate, and hard) and stocking type (mob vs sustained). In mob grazing plots, a larger number of sheep (with actual numbers depending on available feed-on-offer of the moderate

No.	Species	Cultivar	Sowing rate (kg ha^{-1})
Legumes			
1	*Coronilla varia*		0.02
2	*Lotus corniculatus*	Cascade, Maitland	0.9
3	*Lotus pedunculatus*	Grasslands Maku	2.1
4	*Lotus corniculatus* × *L. pedunculatus*	G4712	2.1
5	*Lupinus polyphyllus*	Russell	2.1
6	*Medicago sativa*	Saranac	1.8
7	*Trifolium ambiguum*	Prairie	2.1
8	*Trifolium hybridum*	Tetra, local	0.8
9	*Trifolium medium*		1.9
10	*Trifolium pratense*	Grasslands Pawera	1.1
11	*Trifolium repens*	Grasslands Huia	0.3
Grasses			
12	*Agrostis capillaris*		0.6
13	*Arrhenatherum elatius*		0.2
14	*Bromus willdenowii*	Grasslands Matua	0.2
15	*Bromus scoparius*		1.0
16	*Cynosurus cristatus*		1.3
17	*Dactylis glomerata*	Grasslands Apanui	5.0
18	*Festuca arundinacea*	Grasslands Roa	4.7
19	*Festuca rubra* ssp. *commutata*		1.4
20	*Holcus lanatus*	Massey Basyn	1.2
21	*Lolium perenne*	Grasslands Nui	3.5
22	*Lolium* × *hybridum*	Grasslands Ariki	3.5
23	*Phalaris aquatica*	Grasslands Maru	4.7
24	*Phleum pratense*	Grasslands Kahu	1.3
Herbs			
25	*Sanguisorba minor ssp. muricata*		3.0

Table 3.1: Species over-sown on the study site in 1982, with sowing rates.

plot) were introduced to plots for 3–4 days, while sustained grazing plots received a lower number of sheep for a longer period (e.g., several weeks). Only plots corresponding to the mob stocking type were considered.

Grazing intensity levels corresponded to a 1:2:4 sheep-grazing days ratio in the years 2–4 of the experiment and 2:3:4 in subsequent years. Plots were always grazed in groups of three, corresponding to the three mob-stocked grazing intensity levels per whole plot. For each grazing event (i.e., when vegetation had reached approximately 30 cm in height), sheep numbers were adjusted based on available feed-on-offer of the moderate grazing treatment, using expert knowledge (D. Scott). The duration of grazing was the same for all three plots, but was adjusted based on residual bulk of the moderate grazing treatment (i.e., height of 1–2 cm).

The grazing intensity treatment is relative (within each whole plot) and not absolute, because actual sheep numbers can vary among whole plots depending on forage availability. Consequently, the absolute amount of vegetation biomass consumed by sheep over a given period is strongly correlated with aboveground net primary production (ANPP; $r = 0.995$, $P \leq 0.0001$; see Chapter 5 for details on ANPP estimates). The close relationship between primary production and herbage consumption was a design feature, not an artefact. In fact, it is a key element of the experiment that increases its realism and ecological relevance because herbivore biomass, consumption and production are tightly correlated to primary production in ecosystems (McNaughton et al., 1989). Grazing treatments occur in the period November-May each year. Depending on the fertiliser level, there were between 4–9 grazing cycles during the sampling period (October 2007–April 2009). Sheep carrying capacities among the different experimental treatments have been analysed and modelled in previous work (Scott, 2000c, 2002). Grazing occurs in the period November–May.

In addition to the 30 experimental plots described above (i.e., two blocks $\times$ five fertiliser treatments $\times$ three grazing intensities), two 8$\times$50-m control plots were added in an area directly adjacent to the experiment. These two plots had not been sown, fertilised, or irrigated. Moreover, they had not been grazed since at least 1981, and only lightly grazed before then, at the same intensity as the rest of the experimental site prior to this experiment being

initiated.

3.3.3 Vegetation Sampling

For the present study, an additional factor, vegetation sampling method (two levels: visual ranking vs percent cover), was added to this experimental design. The output from the two methods were paired per plot. Since sampling method was nested within plots, this effectively transformed the experiment into a split-split-plot design for the purpose of statistical analyses.

Visual Ranking Method

For the visual ranking method, the sample unit was the entire 8×50-m plot in which the ten-most abundant vascular plant species were visually ranked according to standing biomass (Scott, 1989). The ratio of abundance between the fifth- and first-ranked species (the "5:1 ratio", hereafter $R_{5,1}$) was also estimated (Scott, 1989). Once all 30 plots were sampled, the whole procedure was repeated two additional times, but only for the first five-most abundant species in each plot. In order to derive species relative abundances p_i from ranks r_i, relative abundances from ranks for each of the three rounds, Scott's (1989) suggestion to use the geometric series was followed:

$$p_i = (1 - k)\, k^{(r_i - 1)}$$

where $k = \sqrt[4]{R_{5,1}}$. $R_{5,1}$ is used to determine the gradient of the linear relationship between log(abundance) and rank, thereby enabling estimation of the relative abundances of all species (Scott, 1989). For statistical analyses, results of the three rounds were averaged, and only the first five-most abundant species per plot were kept. The first five-most abundant species in each plot together accounted for 79.7–99.7% of abundance, such that changes in vegetation composition should be well reflected by considering the five-most abundant species only (see Section 3.3.4 on page 40, where this is assumption is tested).

Percent Cover Method

For the percent cover method, 20 1×1-m quadrats (sample units) were randomly positioned along two longitudinal transects in each plot. Transects were 3 m apart from each other and 2 m from the closest fence to avoid edge effects. Cover (i.e., vertical projection of canopy, including living and non-living components) of all vascular plant species present in each 1×1-m quadrat was recorded using a seven-point semi-quantitative scale (1, $< 0.1\%$; 2, 0.1–0.9%; 3, 1–5%; 4, 6–25%; 5, 26–50%; 6, 51–75%; 7, 76–100%). Mean percent cover per species per plot was calculated by taking the median of the cover class for each species in all 20 quadrats, then averaging across these quadrats. Because percent cover is estimated individually for each species, and because canopy projections of different species can overlap, mean percent cover could exceed 100%. Species present within the entire plot but in none of the individual 20 1×1-m quadrats were assigned the lowest possible cover value (i.e., the median of cover class 1, divided by 20). Percent cover data per plot were transformed to relative abundances by dividing the percent cover of each species by the sum of percent cover values for all species present. As with the visual ranking method, only the first five-most abundant species per plot were kept for analyses. In each plot, these first five-most abundant species together accounted for 81.9–99.6% of abundance.

For both methods, sampling was undertaken by the same observer (E. Laliberté) in year 26 of the experiment (early November 2008). Methods were followed independently and not simultaneously, such that all plots were first sampled using the percent cover method before moving on to the visual ranking method. Sampling all 30 plots with the percent cover method took three consecutive days, while the visual ranking method was done in one afternoon (about one hour per round, three hours total). Temporal separation of sampling methods (and the fact that the percent cover field data were deliberately not consulted prior to visual ranking) minimised the chances of the results of one method influencing the other.

3.3.4 Statistical Analyses

To see whether changes in vegetation composition should be well reflected by considering the five-most abundant species only, data from the percent cover method (which included all plant species) were used to compare the first 20 principal coordinates of Modified-Gower distance matrices (base 10; Anderson, 2006) computed from the full data set (all species) and the reduced data set (only the five-most abundant species per plot) through a Procrustes test (Peres-Neto and Jackson, 2001). These first 20 principal coordinates represented 100% and 99.82% of the variation of the reduced and full data sets, respectively. The Procrustes test was run using 999 permutations with the `protest` function of the `vegan` package (Oksanen et al. 2010) for R (R Development Core Team, 2010). There was a strong and highly significant Procrustes correlation between the two multivariate data sets ($r_{Proc} = 0.850$, $P = 0.001$), suggesting that only considering the first five-most abundant species should reflect well changes in vegetation composition.

The Pearson correlation coefficient r was computed between the relative abundance data (ranging from 0 to 100) collected with the visual ranking method and the data collected with the percent cover method, after $\log(x+1)$ transformation. Major axis regression (with no intercept) was also used on the $\log(x + 1)$ transformed data and tested whether the slope differed from 1 (Warton et al., 2006). For the eight-most abundant plant species across all treatments, biplots were used for visual comparisons of the observed data against the 1:1 line.

The effects of fertiliser, grazing intensity, and vegetation sampling method and their interactions on vegetation composition were tested using permutational distance-based multivariate ANOVA (McArdle and Anderson, 2001). This method is superior to traditional approaches (e.g., MANOVA) for analysing changes in composition because it can be based on any ecologically meaningful distance metric, and not only the Euclidean distance (McArdle and Anderson, 2001). Moreover, P-values are obtained using permutations of the raw data or the residuals, such that no assumptions are made about multivariate normality. This is important because community data rarely meet these assumptions due to heavily positively-skewed distributions and

an over-abundance of zeros (Legendre and Legendre, 1998). Experimental treatments (fertiliser, grazing intensity, and sampling method) were treated as fixed factors, whereas block, whole plot, and plot were treated as random factors.

Three sets of analyses were conducted, each focusing on a different distance/dissimilarity measure. This is particularly important for distance-based analyses because the distance measure can have a strong influence on the results, and because it is useful to explicitly specify the relative importance given to changes in species relative abundances vs changes in presence-absence in the analysis (Anderson et al., 2006). To take this into account, the first test used presence-absence data with the Jaccard dissimilarity (Legendre and Legendre, 1998). The second test used the Modified-Gower distance with base 10 (Anderson, 2006). This distance measure considers an order-of-magnitude change in abundance (e.g., from 1 to 10) equal to a change in presence-absence (i.e. from 0 to 1; Anderson et al., 2006). The third analysis used the same distance measure but with base 2, effectively putting the same weight to a doubling in abundance (e.g., from 1 to 2) as a change in presence-absence (Anderson et al., 2006).

Error structure followed a split-split plot design. As with any split-plot design, such a model has lesser power for detecting treatment effects at the whole plot level (i.e., fertiliser effects), but power progressively increases at the lower levels (i.e., grazing intensity and vegetation sampling method effects) (Gotelli and Ellison, 2004). Underlying assumptions of this split-split plot model are that all interactions involving blocks, whole plots or plots are negligible (Gotelli and Ellison, 2004).

In order to visualise patterns in vegetation composition under the different experimental treatments, non-metric multidimensional scaling (Shepard, 1962; Kruskal, 1964) was used as an ordination method. Non-metric multidimensional scaling returns a two-dimensional biplot that best represents the distance of individual samples (i.e., plots) in multivariate space. Components of variation were used to compare the relative importance of treatments on vegetation composition (Anderson et al., 2008). For fixed factors, these represent the sum of squared fixed effects divided by the appropriate degrees of freedom, and can be directly compared to each other to estimate the rela-

tive importance of treatments from any design, including split-plot designs (Anderson et al., 2008).

One degree-of-freedom (df) contrasts were used for significant terms to further partition significant terms according to a priori hypotheses generated from visual exploration of the non-metric multidimensional scaling plot. The whole-plot analyses used 9999 permutations of the raw data, while 9999 permutations of the residuals under a reduced model were used for the other analyses. Monte-Carlo asymptotic P-values were used when there was a low number of possible unique permutations (Anderson and Robinson, 2003).

To complement the distance-based multivariate ANOVA tests, canonical analysis of principal coordinates (Anderson and Willis, 2003) was used to visualise and interpret significant differences between treatment levels obtained from permutational distance-based multivariate ANOVA when these were not obvious from the non-metric multidimensional scaling biplot. The purpose of canonical analysis of principal coordinates is to find axes in multivariate space that are best at discriminating between a priori groups (Anderson and Willis, 2003). These analyses were conducted in the PRIMER v6/PERMANOVA+ environment (Clarke and Gorley, 2006; Anderson et al., 2008).

3.4 Results

3.4.1 Sampling Method

The species relative abundances collected from both methods were positively associated, though this relationship was not strong ($r = 0.491$ after $\log[x + 1]$ transformation, $P < 0.0001$; Fig. 3.2). Nevertheless, the slope of the major axis regression line did not differ significantly from 1 ($b_{\mathrm{MA}} = 0.997$, Fig. 3.2). The visual ranking method gave greater abundance estimates for lupin (a hybrid of *Lupinus polyphyllus* Lindl.), fescue tussock, and to a lesser degree tall oat-grass (*Arrhenatherum elatius* L.), relative to the percent cover method (Fig. 3.2). It gave slightly lower abundance estimates for mouse-ear hawkweed and zig-zag clover (*Trifolium ambiguum* M. Bieb.) at medium abundance levels (i.e., in the 20-40% range; Fig. 3.2).

Vegetation sampling method, fertiliser, and grazing intensity all had sig-

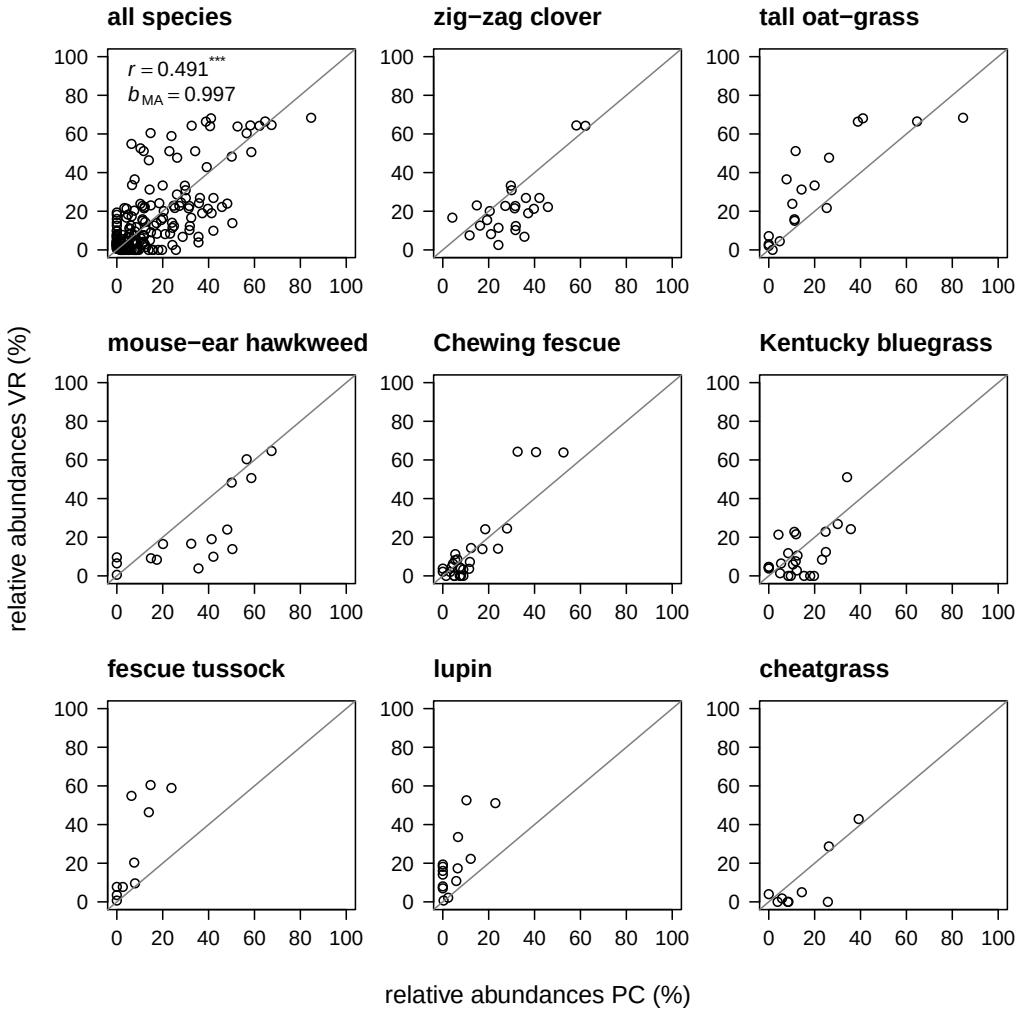

Figure 3.2: Biplots showing the relationships between the visual ranking (VR) method and the percent cover (PC) method. This was done for all species (top left graph) and individually for the eigth-most abundant plant species across all treatments. Graphs for individual species are shown in decreasing order of overall abundance, starting from the top row and moving right. Grey lines indicate the 1:1 relationship. Data from the top-left graph was $\log(x+1)$ transformed to compute the Pearson correlation coefficient r and the major axis regression slope b_{MA} (no intercept). cheatgrass = *Bromus tectorum* L.

Source	Contrasts	*df*	SS	MS	Pseudo-F	P	CoV
Block		1	2.47	0.41	1.30	0.303	0.02
Fert		4	28.34	1.18	3.73	**0.014**	0.43
	0 vs Other	1	17.56	2.93	6.68	**0.003**	0.78
	0 vs 500	1	14.76	2.46	12.11	0.085	1.13
	500 vs Other	1	8.71	1.45	2.24	0.100	0.25
Whole plot error		4	7.61	0.317			0.32
Whole plot total		9	38.42				
Graz		2	2.82	0.57	1.97	**0.047**	0.03
	Low vs Other	1	1.74	0.87	2.67	**0.019**	0.04
	Low vs High	1	1.77	0.89	3.60	**0.029**	0.06
Fert × Graz		8	7.10	0.44	1.54	**0.042**	0.08
Subplot error		10	5.78	0.29			0.29
Subplot total		29	15.17				
Method		1	1.61	1.61	5.77	$<$ **0.001**	0.04
Fert × Method		4	1.26	0.32	1.13	0.301	0.01
Graz × Method		2	0.79	0.40	1.42	0.156	0.01
Sub-suplot error		23	6.42	0.28			0.28
Total		59	63.67				

Table 3.2: Results of permutational distance-based multivariate ANOVA, using the Modified Gower distance base 10 (Anderson, 2006). Error structure followed a split-split-plot design. Fertiliser (Fert) × Grazing intensity (Graz) × Sampling method (Method) interaction was excluded from the model because it had a negative component of variation (CoV), as recommended by Anderson et al. (2008). P-values in bold indicate significant differences at $\alpha = 0.05$ (9999 permutations).

nificant ($P \leq 0.05$) effects on vegetation composition when the latter was expressed using the Modified-Gower base 10 distance (Table 3.2). Importantly, there were no significant interactions involving vegetation sampling method (Table 3.2), indicating that effects of vegetation sampling method on the observed vegetation composition were consistent in size and direction across fertiliser and grazing treatments.

The components of variation (CoV) showed that fertiliser had by far the greatest effect on vegetation composition (CoV = 0.432), its effect being an order-of-magnitude greater than sampling method (CoV = 0.044), with the latter accounting for almost twice as much variation in vegetation composition as grazing intensity (CoV = 0.028; Table 3.2).

The differences in vegetation composition between sampling methods identified from the main test (Table 3.2) were not obvious from the non-metric multidimensional scaling plot (Fig. 3.3a). Therefore, canonical analysis of principal coordinates (Anderson and Willis, 2003) was used to find the

canonical axis that best discriminated plots according to sampling method. Of all plant species, lupin had the greatest Pearson correlation with this canonical analysis of principal coordinates axis ($r = -0.293$), indicating that it was more abundant in plots sampled under the visual ranking method. This reinforced the previous finding that the visual ranking method gave higher estimates of the abundance of lupin relative to the percent cover method (Fig. 3.2).

3.4.2 Treatment Effects

The strong fertiliser effect could be readily identified from the non-metric multidimensional scaling plot (Fig. 3.3a), with zero-fertiliser plots (black symbols) being clearly separated from fertilised ones in ordination space. There was also an apparent distinction of high fertiliser/irrigated suplots (white symbols) from those of other fertiliser levels, while plots receiving 50, 100, or 250 kg ha^{-1} yr^{-1} of superphosphate did not appear to differ from each other in terms of vegetation composition. *A priori* contrasts (Table 3.2) revealed significant differences in vegetation composition between the zero-fertiliser plots and the other ones ($P = 0.003$), but not of high fertiliser/irrigated plots from the others ($P = 0.100$). Very similar results were obtained using the other two distance measures (results not shown).

Species showing a Pearson correlation $r > 0.5$ with any of the two non-metric multidimensional scaling axes were added as a vector overlay on the non-metric multidimensional scaling plot (Fig. 3.3b); this cut-off was used for improving visual clarity, by eliminating species showing weaker relationships with the non-metric multidimensional scaling axes. This indicated that along the first non-metric multidimensional scaling axis, zero-fertiliser plots were characterised by a greater abundance of mouse-ear hawkweed, fescue tussock, blue tussock (*Poa colensoi* Hook.f.), and *Pyrranthera exigua* (Kirk) Zotov, while fertilised plots contained a greater abundance of zig-zag clover and Kentucky bluegrass (*Poa pratensis* L.; Fig. 3.3). A notable feature of the second non-metric multidimensional scaling axis was that high fertiliser/irrigated plots were characterised by a greater abundance of Chewing fescue (*Festuca rubra* ssp. *commutata* Gaudin), while they contained little lupin relative to

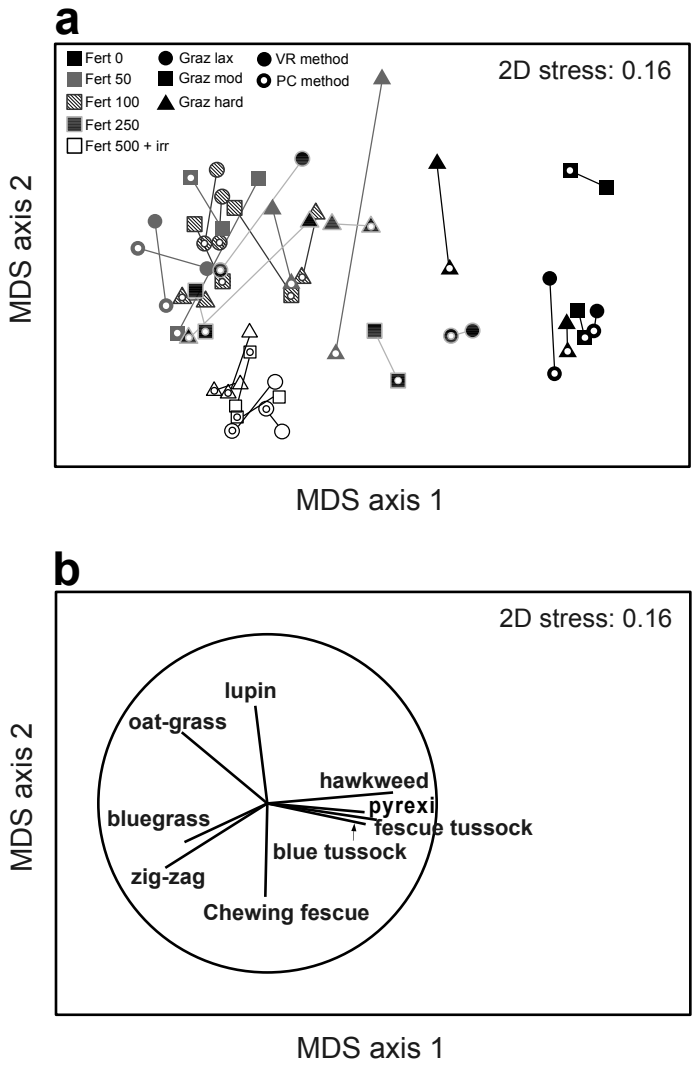

Figure 3.3: Non-metric multidimensional scaling of the vegetation composition data, showing (**a**) subplots and (**b**) species. The Modified-Gower distance with base 10 (Anderson et al. 2006) was used. In (**b**), the length and direction of each vector (species) indicates the strength and sign of the correlation between the two non-metric multidimensional scaling axes. Only species showing a Pearson correlation $r > 0.5$ with any of the two non-metric multidimensional scaling axes are shown. Symbols linked by lines indicate the same subplot sampled under the percent cover (PC) method (white dots) or the visual ranking (VR) method (no dots). pyrexi = *Pyrranthera exigua* (Kirk) Zotov.

other fertilised plots (Fig. 3.3).

There was a significant fertiliser × grazing intensity interaction ($P = 0.042$; Table 3.2), suggesting that effects of grazing on vegetation composition were not consistent across fertiliser levels. However, *post hoc* pairwise comparisons did not indicate significant differences due to grazing among the different fertiliser levels (results not shown), possibly because of low statistical power. Patterns in the non-metric multidimensional scaling plot (Fig. 3.3a) suggest that this significant interaction may result from grazing showing little effect on vegetation composition in high fertiliser/irrigated plots relative to other fertiliser levels. In particular, among plots receiving 100 kg ha^{-1} yr^{-1} of superphosphate, those under hard grazing (Fig. 3.3a; triangles) appeared to occupy a distinct location in ordination space compared with those under moderate (Fig. 3.3a; squares) or lax grazing (Fig. 3.3a; circles).

The main grazing intensity effect was not obvious from the non-metric multidimensional scaling plot (Fig. 3.3a). Therefore, canonical analysis of principal coordinates was used to find the linear combinations of principal coordinates that best discriminated plots under different grazing intensities. The resulting canonical analysis of principal coordinates biplot (Fig. 3.4a) showed that differences were between the lax-grazing treatment and the other two grazing levels, which was confirmed by a significant *a priori* contrast (Table 3.2). A vector overlay of all species showing a Pearson correlation $r > 0.3$ was added to the canonical analysis of principal coordinates biplot, but no species showed particularly strong associations with any of the non-metric multidimensional scaling axes, which was reflected by the short length of all vectors (Fig. 3.4b). The $r > 0.3$ cut-off was chosen here because of relatively weak associations of individual species with the canonical analysis of principal coordinates axes. Nevertheless, there was a tendency (as seen along canonical analysis of principal coordinates axis 1) for lax-grazing plots to have greater abundance of tall oat-grass, timothy (*Phleum pratense* L.), and Chewing fescue, while moderately- and highly-grazed ones had a greater abundance of Kentucky bluegrass and zig-zag clover (Fig. 3.4).

Very similar results were obtained when only presence-absence data (using the Jaccard dissimilarity) were considered as well as when vegetation composition was expressed using the Modified-Gower base 2 distance (results not

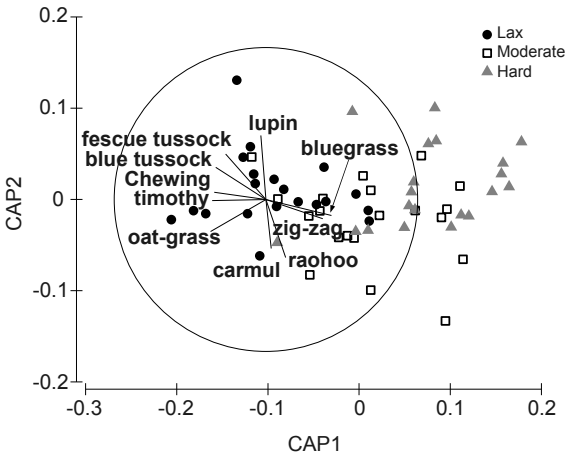

Figure 3.4: Canonical analysis of principal coordinates highlighting the differences in vegetation composition (Modified-Gower base 10 distance) among (**a**) subplots under different grazing intensities. (**b**) Vectors represent the species showing a Pearson correlation $r > 0.3$ with any of the two canonical analysis of principal coordinates axes. carmul = *Carex muelleri* Petrie; raohoo = *Raoulia hookeri* Allan.

shown), despite the latter putting a great weight on differences in species relative abundances. The only notable differences between the results obtained from the different distance/dissimilarity measures was the absence of significant grazing and fertiliser × grazing effects when only presence-absence data were considered ($P = 0.190$). The fertiliser × grazing interaction was also marginally non-significant ($P = 0.059$) when the Modified-Gower base 2 distance was used.

3.5 Discussion

Both vegetation sampling methods gave qualitatively similar results, although the visual ranking method gave greater estimates of the abundance of lupin, fescue tussock and tall oat-grass, and slightly gave lower estimates of the abundance of mouse-ear hawkweed and zig-zag clover, relative to the percent cover method. Despite these differences, the effect of sampling method on observed vegetation composition was consistent among fertiliser and grazing treatments. This suggests that both sampling methods were equally good

at detecting management effects on vegetation composition in these grasslands. This is reinforced by the fact that modifying the relative importance given to changes in presence-absence or relative abundances by using different distance measures had little effect on the results. Even though sampling method did influence the observed vegetation composition, this effect was an order-of-magnitude smaller than the main fertiliser effect. In addition, grazing effects were still detected irrespective of sampling method, despite grazing having subtler effects on the observed vegetation composition than the sampling method itself.

Differences between sampling methods were primarily driven by lupin, a tall species relative to the other species. The percent cover method gave lower abundance estimates for this species compared to the visual ranking method. It is also notable that the other two species which were underestimated by the percent cover method (e.g., tall oat-grass and fescue tussock) were also tall, while species which were over-estimated by the percent cover method (e.g., zig-zag clover and mouse-ear hawkweed) were relatively small in size. These differences between the two methods are likely due to the fact that the visual ranking method uses standing biomass as the measure of "abundance" (Scott, 1989) while the percent cover method uses ground projection of canopy cover. Clearly, in communities where species differ greatly in height or life form (e.g., open shrublands), large differences between results obtained with the visual ranking and the percent cover method may be expected strictly because of the respective focus of each method on different measures of "abundance". However, in this case all plots were dominated by herbaceous vegetation, and differences between the two methods were not large enough to influence their ability to detect changes in vegetation composition from experimental treatments.

In this study, the two vegetation sampling methods compared were both based on visual estimation, either of species standing biomass or of canopy cover. Recently, ground-based or aerial digital imagery has been proposed as more rapid and cost-effective alternatives to visual estimation of vegetation cover in rangelands (Seefeldt and Booth 2006). However, these new digital technologies can currently only be used to measure overall plant cover (Seefeldt and Booth, 2006) or to measure the relative cover of different plant

life forms (e.g., grasses, forbs, and shrubs; Luscier et al., 2006), but not individual species. The emerging field of "airborne spectranomics" may eventually allow distinction at the species level from aerial or satellite images (Asner and Martin, 2009), but this is still far from being available as a rangeland monitoring tool. Until then, ground-based estimation of plant species abundances remains the best-available tool for monitoring changes in rangeland vegetation composition following the adoption of new management strategies. Direct measurement of plant biomass by species has been widely used in grassland/rangeland assessment and arguably remains the most accurate method, but faster and more cost-efficient visual estimation methods often need to be used. Of the two visual methods compared here, the visual ranking method was as good as the percent cover method at detecting changes in vegetation composition following rangeland development, yet was about an order-of-magnitude faster (i.e., $\sim$ 3 hours for visual ranking vs $\sim$ 30 hours for percent cover).

Although the primary interest of this study was to test for differences in observed vegetation composition under different sampling methods, the results showed a strong effect of fertiliser and much a smaller, but still significant, effect of grazing intensity. Plots receiving no fertiliser were characterised by a greater abundance of mouse-ear hawkweed, blue tussock, fescue tussock, and *Pyrranthera exigua* compared to fertilised plots. These species are characteristic of the vegetation prior to establishment of the experiment (Scott, 1999). Within fertilised plots, those receiving 500 kg ha^{-1} yr^{-1} of superphosphate and irrigation contained more Chewing fescue and less lupin. While grazing intensity has been shown to cause strong threshold changes in vegetation composition of Mongolian rangelands (Sasaki et al., 2008), these results show instead a strong threshold responses in vegetation composition following the application of superphosphate, but a much smaller effect of grazing intensity.

Uncommon species were purposefully excluded from the analyses since the visual ranking method aimed at characterizing vegetation composition by ranking the 10-most abundant species only in each plot. Monitoring native and overall species richness in rangelands is important from a conservation perspective (e.g., Symstad et al., 2008; Godínez-Alvarez et al., 2009),

especially since species richness has been shown to vary under changing management in New Zealand rangelands (Norton et al., 2006). Nevertheless, vegetation composition, as expressed by the dominant species, is still useful for most agronomic applications (e.g., Scott, 2007). Moreover, as predicted by the mass-ratio hypothesis (Grime, 1998), vegetation effects on ecosystem biogeochemical processes may be primarily driven by the most-abundant species (Mokany et al., 2008), such that excluding rare species from the analysis may not drastically alter the ability to assess vegetation feedbacks on ecosystem-level processes.

Most comparisons of vegetation sampling methods in rangelands have focused on species richness (e.g., West and Reese, 1991; Stohlgren et al., 1998; Godínez-Alvarez et al., 2009) and/or the cover of individual species or functional groups (Prosser et al., 2003; Symstad et al., 2008), but none had yet focused on changes in vegetation composition as was done here. In this study, the percent cover and the visual ranking methods were used to sample only the most-abundant species in each plot, but both methods could be extended to more detailed biodiversity surveys. However, if the focus is to detect main changes in vegetation composition from the perspectives of rangeland agronomy or rangeland ecological functions, the results from this study show that the visual ranking method is as good as the percent cover method, despite the latter being a more field-intensive method using repeated sub-sampling.

3.6 Conclusions

The purpose of this study was to compare a rapid visual ranking vegetation sampling method (Scott, 1989) to a more field-intensive percent cover method based on repeated sub-sampling with many quadrats. Both methods were equally good at detecting changes in vegetation composition under different fertiliser and grazing intensity regimes. The visual ranking method gave higher abundance estimates for lupin relative to the percent cover method, most likely because the measure of "abundance" differed between methods (standing biomass for visual ranking, and canopy cover for percent cover) and because of the greater height lupin relative to other species. However,

differences between methods on observed vegetation composition were very small compared to the main effect of fertiliser. The much greater efficiency of the visual ranking method compared to the percent cover method (i.e., about 10 times faster in the present study) supports the use of the visual ranking method as a rapid yet powerful method for detecting changes in vegetation composition following rangeland development, at least in grasslands.

Chapter IV

Trait-Based Plant Community Assembly Under Long-Term Shifts in Soil Resource Availability and Grazing Intensity[1]

4.1 Summary

Soil resource availability and disturbance (i.e., destruction of live biomass) are widely recognised as key drivers of plant community structure. In this Chapter, trait-based plant community assembly is studied in a 27-year experiment where a common species pool was sown into semi-arid grasslands in New Zealand, after which soil resource availability (five levels of P/S fertiliser and irrigation) and disturbance (three levels of sheep grazing intensity) were manipulated. Shifts in trait distributions are explored and compared to null models, and a maximum entropy approach is used to quantify the direction and strength of selection on each trait. Species were primarily differentiated along a nutrient acquisition–conservation trade-off axis corresponding to traits promoting rapid growth (e.g., high leaf [N] and specific leaf area) vs those promoting long leaf lifespan. Species with leaf attributes that reduce nutrient losses held a long-term advantage under the lowest soil resource availability, whereas those associated with a rapid growth rate quickly became dominant under soil resource addition. There was a trend towards an increasingly positive selection for species with thinner leaves under greater soil resource availability, which may reflect a strategy to maximise specific leaf area without sacrificing leaf density, and thus maintain leaf structural

[1] This Chapter is currently under review:
Laliberté, E., Shipley, B., Norton, D. A. and Scott, D. (in review). Trait-based plant community assembly under long-term shifts in soil resource availability and grazing intensity. *Ecological Monographs*.

defenses under grazing. Moreover, greater leaf [S] and the ability to symbiotically fix atmospheric N conferred greater fitness under soil resource addition. Greater plant height, thinner leaves, and higher leaf [N] conferred greater fitness with lower grazing intensity, but thinner leaves became less advantageous under higher grazing intensity. There was strong evidence for trait-based filtering at the highest soil resource availability, where all short species with a nutrient-conserving strategy were competitively excluded. In contrast, under the lowest soil resource availability, species relative abundance was markedly over-dispersed along particular trait axes (e.g., leaf [P]), suggesting limiting similarity with respect to strategies of resource acquisition and use. These results highlight the importance of considering species functional differences to understand how plant communities react to increases in soil resource availability and the intensity or frequency of disturbance, two important but often inseparable components of land-use change.

4.2 Introduction

Given a common regional species pool, what determines the composition of local communities? Answering this fundamental question has been a major goal of community ecology since its beginnings (Clements, 1916; Gleason, 1926). In an effort to understand the determinants of bird species composition on islands of varying sizes, Diamond (1975) pioneered the concept that "assembly rules" might govern local community composition. While this work generated much interest, as well as some criticism (e.g., Connor and Simberloff, 1979), one important limitation was the focus on taxonomic identity and species-based assembly rules. This prevented any generalizations from one system to other systems with differing species pools.

More recently, phylogenetic patterns at the community level have been used to infer processes governing community assembly (Webb et al., 2002; Swenson et al., 2006; Helmus et al., 2007; Emerson and Gillespie, 2008; Cavender-Bares et al., 2009), often with the implicit assumption that phylogenetic distances reflect ecologically relevant species differences (but see Prinzing et al., 2008; Kraft and Ackerly, 2010). However, an explicit focus on underlying functional traits is essential to make community ecology

a more general, predictive science (Keddy, 1990; McGill et al., 2006; Webb et al., 2010). Indeed, the ecological processes at play during community assembly do not act on species *per se*, but instead on individuals possessing different morphological or physiological attributes that directly or indirectly influence their fitness. Hence, functional traits can be broadly defined as sub-organismal or organismal characters affecting the growth and probabilities of survival and reproduction in different environments (Violle et al., 2007; Shipley, 2010b).

Trait-based community assembly was initially viewed as a series of successive abiotic or biotic "filters" that exclude unsuitable strategies from those found across the entire available species pool (Keddy, 1992; Díaz et al., 1998). The successive set of filters thus represents the trait-based rules that govern community assembly at a local site (Keddy, 1992). Despite its conceptual appeal, the strict notion of "filters" invokes a series of binary decisions that dictate whether a species will be present or not at a site, yet says nothing about its expected abundance (Shipley, 2010b; Cornwell and Ackerly, 2010). For instance, both the amount of soil resources available and the level of disturbance strongly structure local communities (Grime, 2002), yet these continuous factors do not simply allow or prevent particular ecological strategies from occurring at a local community. In an effort to modify Keddy's (1992) original concept into a more probabilistic view of trait-based community assembly, Shipley (2010b) used the analogy of a "stochastic filter", which specifies the expected relative abundance of a species rather than its presence or absence. Under this new analogy, the relative abundances of species are constrained by their functional attributes such that species possessing attributes conferring greater fitness become more abundant on average, but with a strong stochastic component that recognises the importance of chance events affecting community composition. It follows that trait-based community assembly reflects the process of natural selection acting on reproductively isolated groups of individuals (i.e., species), but on an ecological rather than an evolutionary timescale (Keddy, 1992; Shipley, 2010b).

If trait-based assembly rules exist, then non-random patterns of species functional attributes should be found within communities. To date, most research on trait-based community assembly has been directed towards this

goal. Such studies have been undertaken with bird (Ricklefs and Travis, 1980; Lockwood et al., 1993; Moulton and Pimm, 1987), rodent (Hopf and Brown, 1986), fish (Mason et al., 2007; Ingram and Shurin, 2009), and plant communities (Weiher et al., 1998; Stubbs and Wilson, 2004; Kraft et al., 2008; Cornwell and Ackerly, 2009; Rada, 2000; Kraft and Ackerly, 2010). Classical competition theory states that there is a limit to how similar co-occurring species can be, because two species competing for the same resources cannot stably co-exist (MacArthur and Levins, 1967). Based on this principle, some authors have tested for over-dispersion (e.g., even spacing) of species distributions in functional trait space, emphasizing the role of competition during community assembly (Stubbs and Wilson, 2004). Others have instead focused strictly on environmental filtering as the main trait-based assembly process (Díaz et al., 1998; Lebrija-Trejos et al., 2010), focusing on under-dispersion (e.g., restricted range or clumping) of functional attributes (Weiher and Keddy, 1995).

Plant traits do not vary at random among species but covary along major axes of functional variation or trade-offs (Grime et al., 1997; Wright et al., 2004; Díaz et al., 2004; Shipley et al., 2006a; Maire et al., 2009), leading to distinct ecological strategies (Grime, 1974; Westoby et al., 2002; Ackerly, 2004). It is increasingly recognised that the biotic and abiotic processes that drive community assembly are not mutually exclusive, but can instead act on different axes of functional variation (Weiher et al., 1998; Suding et al., 2003; Gross et al., 2007; Kraft et al., 2008; Ingram and Shurin, 2009), or sometimes on the same axis (Cornwell and Ackerly, 2009). Testing for non-random patterns of trait over- and under-dispersion can thus provide insights on the filtering processes that are structuring communities. Nevertheless, despite their merits, such pattern-seeking analyses cannot yield explicit trait-based assembly rules that lead to quantitative predictions about the composition of local communities (Keddy and Weiher, 1999). This has led Weiher et al. (1998) to conclude that "the patterns caused by community assembly [are] abundantly evident, but the rules themselves [remain] elusive".

Recently, an alternative approach has been developed that yields quantitative trait-based assembly rules and predictions of species relative abundances (Shipley et al., 2006b; Shipley, 2010b) and has generated much in-

terest and debate (McGill, 2006; Roxburgh and Mokany, 2007; Marks and Muller-Landau, 2007; Shipley et al., 2007; Haegeman and Loreau, 2008; Shipley, 2009b; Haegeman and Loreau, 2009; Shipley, 2009c; He, 2010; Roxburgh and Mokany, 2010; McGill and Nekola, 2010; Shipley, 2010a). If natural selection constrains the composition of a local community in such a way that the individuals of species possessing favourable functional attributes in a particular environment (i.e., attributes that confer greater fitness) become more abundant, then predictable community-level patterns (representing the "constraints" imposed by community assembly processes), should emerge (Shipley, 2010a,b). Shipley et al. (2006b) defined these "constraints" as community-aggregated traits (Garnier et al., 2004; Díaz et al., 2007a), which are best understood as the trait values of an average individual or biomass unit chosen at random from a community (Shipley, 2010b); recent convention seems to prefer the term "community-weighted mean" and this convention will be followed hereafter. For example, under low rainfall and low nutrient availability, plant communities are expected to be dominated by individuals or species with lower specific leaf area and higher leaf density (Cunningham et al., 1999). However, given a known species pool, a very large (potentially infinite) number of different community compositions (i.e., combinations of varying species relative abundances) can adequately meet the criteria of any set of specified constraints expressed as community-weighted traits (Shipley, 2009c). One solution to this problem, provided by Information Theory and Bayesian statistics is to find, among the very large set of possible community states, the one that maximizes Shannon's (1949) index of information entropy or relative entropy. This decision is justified by the fact that this particular community composition is the only one that is both consistent with all stated constraints and that does not imply any additional constraints (Jaynes, 2003; Shipley et al., 2007).

In order to identify trait-based assembly rules, the relative importance of different traits in determining relative abundance needs to be measured, as well as the strength and direction of selection in determining relative abundance, before testing their significance. Provided that good predictions of the observed relative abundances can be derived from the observed constraints (i.e., observed community-weighted traits), then particular parameters (i.e.,

the λ-values, or weights on the traits) of the maximum entropy (maxent) model (Shipley et al., 2006b) can be used to assess the relative importance of different traits in determining species relative abundances, and enable us to find a parsimonious set of the most important traits (Shipley, 2010b; Sonnier et al., 2010a). Importantly, in doing so the relative importance of different traits can be compared across different environments.

Grime (2002) argued that trait-based community assembly would be best studied by constructing synthetic communities from a common species pool, experimentally altering environmental conditions and/or disturbance regimes, and documenting changes in composition as communities adjusted to the altered conditions. Ideally, such experiments should be of a sufficiently long duration to allow time for communities to adjust to their new, experimentally-altered conditions. In this Chapter, trait-based plant community assembly is studied in a 27-year experiment conducted in New Zealand grasslands, where a common species pool of 25 plant species was sown into the resident vegetation within a $\sim$ 3-ha area in 1982, after which soil resource availability and grazing intensity were experimentally manipulated (Scott, 1999). This experiment allowed us to explore in a controlled setting how these two factors together drive long-term plant community assembly.

Specifically, the following questions are asked:

1. What are the relationships among the set of measured plant functional traits in this system, and can primary axes of functional variation be identified?

2. How are trait distributions altered following long-term shifts in soil resource availability and grazing intensity?

3. What are the most important plant functional traits in determining abundance in these grasslands?

4. How does the selective advantage of different traits vary across the different experimental treatments?

4.3 Materials and Methods

4.3.1 Study Area and Study Site

A detailed description of the study area and study site is given on page 34.

4.3.2 Experimental Design

A detailed description of the experimental design is given on page 34.

4.3.3 Vegetation Sampling

Visual ranking

Every year since 1983, the ten-most abundant plant species in each plot were visually ranked according to standing biomass (Scott, 1989). The abundance ratio between the fifth- and first-ranked species ($R_{5,1}$) was also estimated (Scott, 1989). In order to derive species relative abundances p_i from ranks r_i, Scott's (1989) suggestion to use the geometric series was followed:

$$p_i = (1 - k)\, k^{(r_i - 1)}$$

where $k = \sqrt[4]{R_{5,1}}$. Plots were sampled at least three times on different days, and abundances from the three rounds were averaged. These data were used subsequently in this study to explore temporal patterns in community-weighted traits, but were not used with maxent models.

Percent cover

Sampling of all vascular plant species present within each plot (Table 4.1) was also undertaken in November 2007. Twenty 1×1-m quadrats were randomly positioned along two longitudinal transects (10 quadrats per transect) in each plot. Transects were 3 m apart from each other and 2 m from the closest fence. Cover (i.e., vertical projection of canopy, including living and non-living components) of all vascular plant species present in each 1×1-m quadrat was recorded using a seven-point semi-quantitative scale (1, ≤ 0.1%; 2, 0.1–0.9%; 3, 1–5%; 4, 6–25%; 5, 26–50%; 6, 51–75%; 7, 76–100%). Mean percent cover per species per plot was calculated by taking the median of

the cover class for each species in each of the 20 quadrats, then averaging across these quadrats. Because percent cover is estimated individually for each species, and because canopy projections of different species can overlap, total percent cover could exceed 100%. Species present within the entire plot but not in the 20 individual 1×1-m quadrats sampled were assigned the lowest possible cover value (i.e., the median of cover class 1, divided by 20). Percent cover scores per plot were transformed to relative abundances by dividing the percent cover of each species by the sum of percent cover values for all species present. While the results obtained from the visual ranking and percent cover sampling methods are only moderately correlated ($r = 0.491$, $P \leq 0.001$; see Chapter 3), both methods detect consistent differences in plant community structure among fertiliser and grazing treatments (Chapter 3). These data were used to test for differences in community-weighted traits and species richness, to explore trait over- and under-dispersion, and for maximum entropy models.

4.3.4 Plant Functional Traits

Morphological and Chemical Traits

A set of 14 functional traits (Table 4.2) was selected from the standard lists of Cornelissen et al. (2003) and Garnier et al. (2007); these traits have been identified as traits that typically predict species responses to environmental change and their effects on ecosystem processes, while still being easily measurable across a wide range of species (Weiher et al., 1999; Cornelissen et al., 2003; Garnier et al., 2007). Specific leaf area (SLA), leaf area (LA), and leaf dry matter content (LDMC) were measured on at least 10 individuals per plant species (spread among the five fertiliser treatments, with a minimum of two individuals per fertiliser level), following the standardised methodology of Garnier et al. (2001). A composite sample of 10 individuals per species (spread among the five fertiliser treatments) was used for leaf nutrient analyses (leaf nitrogen concentration [LNC], leaf carbon concentration [LCC], leaf phosphorous concentration [LPC], and leaf sulphur concentration [LSC]; Table 4.2). Leaf sulphur concentration (LSC) was added to the list because S has been shown to be a key limiting nutrient in these grassland systems

Code	Species	Family	N / E	Sowing rate (kg ha^{-1})*	Mean abun. (%)	Range abun. (%)
Aa	*Aphanes arvensis*	Rosaceae	E	-	0.13	0–2.03
Ac	*Agrostis capillaris*	Poaceae	E	0.6	2.27	0–14.50
Ae	*Arrhenatherum elatius*	Poaceae	E	0.2	11.54	0–85.81
Am	*Achillea millefolium*	Asteraceae	E	-	0.07	0–2.18
Ao	*Anthoxanthum odoratum*	Poaceae	E	-	0.75	0–9.75
Bb	*Brachyglottis bellidoides*	Asteraceae	N	-	0.01	0–0.06
Bt	*Bromus tectorum*	Poaceae	E	-	4.67	0–28.70
Cbc	*Carex breviculmis*	Cyperaceae	N	-	0.03	0–0.51
Cbi	*Cardamine bilobata*†	Brassicaceae	N	-	0.01	0–0.11
Cbs	*Colobanthus brevisepalus*	Caryophyllaceae	N	-	0.01	0–0.04
Cbu	*Capsella bursa-pastoris*	Brassicaceae	E	-	0.01	0–0.04
Cf	*Cerastium fontanum*†	Caryophyllaceae	E	-	0.01	0–0.05
Cg	*Celmisia gracilenta*	Asteraceae	N	-	0.01	0–0.03
Cm	*Carex muelleri*	Cyperaceae	N	-	0.70	0–6.00
Cp	*Coprosma petriei*	Rubiaceae	N	-	0.24	0–3.17
Cv	*Carmichaelia vexillata*	Fabaceae	N	-	0.26	0–6.43
Dg	*Dactylis glomerata*	Poaceae	E	5	0.74	0–5.23
Ec	*Erodium cicutarium*	Geraniaceae	E	-	0.01	0–0.01
Er	*Elymus rectisectus*	Poaceae	N	-	0.07	0–1.55
Fn	*Festuca novae-zelandiae*	Poaceae	N	-	3.73	0–29.61
Fr	*Festuca rubra*	Poaceae	E	1.4	9.95	0–52.01
Gs	*Geranium sessiliflorum*	Geraniaceae	N	-	0.01	0–0.16
Hc	*Hieracium caespitosum*	Asteraceae	E	-	0.01	0–0.04
Hl	*Holcus lanatus*	Poaceae	E	1.2	0.17	0–1.87
Hpi	*Hieracium pilosella*	Asteraceae	E	-	15.02	0–49.56
Hpr	*Hieracium praealtum*	Asteraceae	E	-	0.01	0–0.20
Lc	*Lotus corniculatus*	Fabaceae	E	0.9	0.01	0–0.01
Lf	*Leucopogon fraseri*	Epacridaceae	N	-	0.39	0–6.93
Lp	*Lupinus polyphyllus*	Fabaceae	E	2.1	2.86	0–24.62
Lr	*Luzula rufa*	Cyperaceae	N	-	0.01	0–0.21
Mp	*Malva parviflora*	Malvaceae	E	-	0.01	0–0.01
Msa	*Medicago sativa*	Fabaceae	E	1.8	0.01	0–0.14
Mst	*Myosotis stricta*	Boraginaceae	E	-	0.04	0–0.38
Oc	*Oreomyrrhis colensoi*	Apiaceae	N	-	0.01	0–0.04
Pc	*Poa colensoi*	Poaceae	N	-	0.77	0–5.88
Pe	*Pyrranthera exigua*	Poaceae	N	-	7.58	0–51.91
Pm	*Poa maniototo*	Poaceae	N	-	0.08	0–0.91
Po	*Pimelea oreophila*	Thymelaeaceae	N	-	0.13	0–1.27
Ppe	*Phleum pratense*	Poaceae	E	1.3	6.66	0–5.01
Pps	*Poa pratensis*	Poaceae	E	-	10.24	0–35.00
Pv	*Pterostylis venosa*†	Orchidaceae	N	-	0.01	0–0.01
Ra	*Rumex acetosella*	Rumaceae	E	-	0.35	0–2.93
Rh	*Raoulia hookeri*	Asteraceae	N	-	0.12	0–3.02
Rs	*Raoulia subsericea*	Asteraceae	N	-	0.01	0–0.28
Sm	*Stackhousia minima*	Stackhousiaceae	N	-	0.02	0–0.21
Sp	*Schenodorus phoenix*	Poaceae	E	4.7	0.46	0–7.90
Ta	*Trifolium ambiguum*	Fabaceae	E	2.1	25.39	0–65.53
Th	*Trifolium hybridum*	Fabaceae	E	0.8	0.01	0–0.27
Tm	*Trifolium medium*	Fabaceae	E	1.9	0.06	0–0.82
To	*Taraxacum officinale*	Asteraceae	E	-	0.30	0–5.05
Tp	*Trifolium pratense*	Fabaceae	E	1.1	0.01	0–0.01
Tr	*Trifolium repens*	Fabaceae	E	0.3	0.04	0–0.75
Vt	*Verbascum thapsus*	Scrophulariaceae	E	-	0.03	0–0.82
Wa	*Wahlenbergia albomarginata*	Campanulaceae	N	-	0.07	0–0.80

Table 4.1: List of the plant species found in the study plots in the 2007–2008 surveys. *Species that were sown at the start of the experiment in 1982; see Table 3.1 for more details. Not all of the 25 sown species were still present in 2007. †These rare species were not considered in some analyses because of incomplete trait data.

(Scott, 2000f). Samples were oven-dried at 60 °C, ground, then sent to a commercial laboratory (Hill Laboratories, Hamilton, New Zealand) for assessment of leaf nutrient concentrations. Because leaf nutrient concentration can vary along soil resource availability gradients, individual samples were used from each fertiliser level for the six species which together accounted for more than 80% of total cover among all plots (Table 4.1), following Garnier et al. (2007). Field-measured traits were measured on all vascular plant species in November 2007, just prior to the start of the grazing treatments for that year.

Height (H) of mature plants was measured from ground level to the tip of the highest photosynthetic organ on at least 10 individuals from each species among the different fertiliser treatments (Garnier et al., 2007), prior to the first grazing in November. Seed mass (SM) and onset of flowering (OF) was measured following Cornelissen et al. (2003) and Garnier et al. (2007), but could not be measured on all species (Table 4.2). Lifespan (LS) and ability to fix atmospheric nitrogen (NF) were assessed using floras (Allan, 1982; Webb et al., 1988; Edgar and Connor, 2000) and electronic databases (Landcare Research, 2008; Peat et al., 2008).

Finally, leaf thickness (LT) was estimated as $(\text{SLA} \times \text{LDMC})^{-1}$ (Vile et al., 2005). This assumes an average leaf density (fresh mass) $\rho_{\text{F}} \approx 1$ kg m^{-3}, which has been shown to be reasonably accurate (Sims et al., 1998; Garnier et al., 1999). This estimate is likely to be biased for species with non-laminar leaves (e.g., the tightly inrolled leaves of *F. novae-zelandiae*). Therefore, the leaf thickness estimate was only used when exploring temporal patterns in community-weighted traits, and in the maxent models (as per Sonnier et al., 2010a), because leaf thickness and LDMC can vary independently along environmental gradients (Witkowski and Lamont, 1991).

Acceptability to Sheep

Since all plots were grazed by sheep (except for the two control plots which had not been grazed since 1982), the relative acceptability of plant species as forage for sheep (AS; Table 4.2) was considered as a potential determinant of plant community assembly. Acceptability was equated with preference

(Johnson, 1980), such that the acceptability of a plant species is assessed as its grazing removal against its abundance or availability. For instance, a species would rate as highly acceptable if it was grazed disproportionally to its availability, and vice-versa. A restricted ordinal scale was used: 1 (low acceptability), 2 (medium acceptability), and 3 (high acceptability). To facilitate classification of plant species into these three categories, existing data from the literature (Cockayne, 1920; Hugues, 1975; Covacevich, 1991) and expert knowledge (D. Scott, personal observation) were used.

4.3.5 Statistical Analyses

Relationships among Species Traits

Principal component analysis (PCA) was used to visualise the inter-relationships among all continuous plant functional traits (Table 4.2) other than onset of flowering, seed mass (because of missing values), and leaf thickness (because of reasons mentioned on the facing page). Correlation biplots (type-II scaling) were used such that the angles between vectors (traits) and principal components reflected their correlations, with a small angle indicating a high correlation (Legendre and Legendre, 1998). In a correlation biplot, projecting the objects at right angles onto a vector approximates their value along this vector (Legendre and Legendre, 1998).

Prior to analyses, some traits (height, LCC, LNC, LPC, LSC, and leaf area) were first log-transformed to make their distributions more symmetric, and thus reduce the influence of species with extreme trait values. Pearson correlation coefficients r were computed between traits and tested for statistical significance. These analyses, and all others in sections below, were conducted in the R environment (R Development Core Team, 2010). Specific analyses described above used the base packages as well as the `bpca` package (Faria and Demetrio, 2009).

Shifts in Community-Weighted Traits

Community-weighted traits were used as "markers" of plant functional composition (Garnier et al., 2004; Díaz et al., 2007b). Community-weighted traits ($\mathbf{C}_{\mathrm{cw}}$) were computed as the weighted trait means for each plot, where

Code	Trait	Type	Units / categories	Range	Number of species
AS	Acceptability to sheep	Ordinal	(1) low; (2) medium; (3) high	1–3	54
H	Plant height*	Continuous	mm	4–564	54
LA	Leaf area	Continuous	mm^2	1–8382	52
LCC	Leaf carbon concentration	Continuous	% (dry weight)	40.2–47.4	51
LDMC	Leaf dry matter content	Continuous	mg g^{-1}	126–498	52
LNC	Leaf nitrogen concentration	Continuous	% (dry weight)	1.1–5.2	51
LPC	Leaf phosphorous concentration	Continuous	% (dry weight)	0.09–0.67	51
LS	Plant lifespan	Ordinal	(1) annual; (2) biennial; (3) perennial	1–3	54
LSC	Leaf sulphur concentration	Continuous	% (dry weight)	0.06–0.58	51
LT†	Leaf thickness (estimate)†	Continuous	mm	0.14–1.20	52
NF	Nitrogen fixation	Binary	(0) no; (1) yes	0–1	54
OF	Onset of flowering	Continuous	Day of year (from July 1)	124–210	49
SLA	Specific leaf area	Continuous	m^2 kg^{-1}	1.8–40.9	52
SM	Seed mass	Continuous	mg	0.03–21.2	42

Table 4.2: List of the functional traits measured on the species. *Height of highest photosynthetic organ at reproductive stage. †Leaf thickness (LT) was not measured but was instead estimated as $(\text{SLA} \times \text{LDMC})^{-1}$. Leaf thickness was only used to explore temporal shifts in community-weighted traits and in the maxent models.

weights are species relative abundances, using the following equation:

$$\mathbf{C}_{\text{cw}} = [c_{ij}] = \sum_{k=1}^{S} o_{ik} t_{kj}$$

where c_{ij} is the weighted mean of trait j from plot i, o_{ik} is the observed relative abundance of species k at plot i (the 2007 vegetation cover data were used), t_{kj} is the value of trait j for species k, and S is the number of species. Community-weighted traits for all leaf chemical traits (LCC_{cw}, LNC_{cw}, LPC_{cw}, LSC_{cw}) were computed using the trait values measured from each fertiliser level (0, 50, 100, 250, or 500 kg ha^{-1} yr^{-1}) because these data were available for the six most abundant species which together comprised >80% of total abundance from all plots (this criterion was assessed with the 2007 vegetation cover data). Doing so partially takes into account intraspecific variation for these traits, which can be important (Garnier et al., 2007; Albert et al., 2010).

Temporal Trends (1981–2008) First, temporal trends in all continuous community-weighted traits were explored (Table 4.2) for the first 27 years of the experiment (i.e., 1981–2008) from the visual ranking vegetation data and the trait data from year 26. For simplicity, in presenting the main trends the 27-year time series was divided into three distinct periods: 0–5 years (the "adjustment" period), 5–20 years (the "middle" period), and 20–27 years (the "post-fertiliser" period). To highlight major temporal trends in the data, generalised additive models (Wood, 2006) were used on community-weighted traits between fertiliser or grazing intensity levels. Because vegetation composition was not assessed prior to the start of the experiment (i.e., in 1981), but only from 1983–onwards, the two control plots from the 2007 vegetation cover data were used as estimates of the starting conditions for all plots. These estimates are necessarily imprecise, because they assume that all plots had exactly the same vegetation composition and because the data were obtained from a different vegetation sampling method (i.e., visual ranking vs vegetation cover) whose results are only moderately positively correlated with each other ($r = 0.491$, $P \leq 0.001$, see Chapter 3). However, community-

weighted traits have little sensitivity to sampling method (e.g., cover vs visual ranking; Lavorel et al., 2008). Moreover, the two control plots should represent reasonable estimates of starting conditions since these have changed little since 1981 (D. Scott, personal observation), while fertiliser treatments led to large and rapid changes in vegetation composition (Scott, 2007). In order to assess these rapid changes, it was judged better to present an approximate estimate than to use a conservative approach and present none at all. In any event, the smoothed temporal trends from the generalised addivite models are phenomenological and exploratory and are treated as descriptive; inferential statistical tests are not conducted on these results. Generalised addivite models were computed in `R`, using the `gam` function in the `mgcv` package (Wood, 2006).

Differences in Community-Weighted Traits at Year 26 Statistical tests of differences in community-weighted traits among fertiliser and grazing intensity treatments were performed on the vegetation cover data at year 26 (i.e., 2007). This was done because (i) these data encompassed all plant species (Table 4.1), not just the most abundant ones (as in the visual ranking data), and (ii) the community-weighted traits from that year were used as the constraints in the maximum entropy models (see next section on the next page). For these analyses, height, LCC, LNC, LPC, LSC, and leaf area were log-transformed prior to computation of community-weighted traits to reduce the influence of species with extreme trait values. SM_{cw} and OF_{cw} were not computed because of missing trait values for a number of species, some of which were relatively abundant (Table 4.2). Principal component analysis correlation biplots were used to visualise the inter-relationships among community-weighted traits in multivariate space, and Pearson correlation coefficients r were computed between the community-weighted traits and tested for statistical significance. Differences in individual community-weighted traits among the different experimental treatments were tested using a split-plot ANOVA model. *Post hoc* Tukey HSD tests were conducted when a significant interaction or main treatment effect was detected. For the purposes of visualisation, abundance-weighted distributions for all continuous traits (Table 4.2) were also plotted; Gaussian kernel density estimates were

used with bandwidths equal to Silverman's (1986) rule of thumb.

Selective Advantage of Traits: Maximum Entropy Models

General description The biological model of community assembly through trait-based habitat filtering (Keddy, 1992; Díaz et al., 1998) states that local abiotic and biotic conditions exert a selective force on individuals with particular functional traits, such that the relative abundances of species found in a local community will be constrained by their trait values. Recently, this biological model has been recently translated mathematically into a maximum entropy (maxent) model by Shipley et al. (2006b) and more completely and rigorously in Shipley (2010b). Only its main features are presented here.

A maxent model seeks to estimate the probabilities $\hat{\mathbf{p}} = [\hat{p_j}]$ of a set of $j = \{1, \ldots, S\}$ possible states, based on a set of macroscopic empirical constraints and a prior probability distribution $\mathbf{q} = [q_j]$. In the context of community assembly, the probabilities $\hat{p_j}$ represent the expected relative abundances of the S species from the regional pool in a local community, and the macroscopic empirical constraints are community-weighted traits (Shipley, 2010b). The prior probabilities q_j are generally a maximally uninformative prior, i.e., a uniform distribution (Shipley et al., 2006b). Alternatively, a more informative prior can be used, such as the relative abundances of species of the regional pool. Doing so can take into account potential differences in propagule pressure exerted by the S species, assuming that propagule pressure is a function of their regional abundance (Shipley, 2010b; Sonnier et al., 2010b).

The general idea behind the maxent model is to find the probabilities $\hat{p}_j$ that maximise the relative entropy:

$$-\sum_{j=1}^{S} p_j \ln\left(\frac{p_j}{q_j}\right)$$

conditional on the empirical or theoretical constraints (Shipley, 2010b). In other words, it is to derive, for a local community, the most "even" predicted relative abundances of all species in the regional pool that respect the specified constraints (in this case, the observed community-weighted trait values)

but without implying any additional constraint, and while taking into account the potential propagule pressure exerted by different species from the regional species pool (estimated by the prior $\mathbf{q}$). The solution to this problem is the Gibbs distribution:

$$\hat{p}_j = \frac{q_j e^{\left(-\sum_{i=1}^{T} \lambda_i t_{ij}\right)}}{\sum_{j=1}^{S} q_j e^{\left(-\sum_{i=1}^{T} \lambda_i t_{ij}\right)}} = \frac{q_j e^{\left(-\sum_{i=1}^{T} \lambda_i t_{ij}\right)}}{Z}$$

where $0 < \hat{p}_j < 1$, S is the number of species in the regional pool, T is the number of traits t, and λ_i is the weight on trait i. $\hat{p}_j$ are solved for by using the Improved Iterative Scaling algorithm of Della Pietra et al. (1997).

One can derive the λ-values (Lagrange multipliers) by solving the linear system of equations:

$$\begin{pmatrix} \ln(\hat{p}_1) \\ \ln(\hat{p}_2) \\ \vdots \\ \ln(\hat{p}_S) \end{pmatrix} = (\lambda_1,\ \lambda_2,\ \ldots,\ \lambda_T) \begin{bmatrix} t_{11} & t_{12} & \ldots & t_{1S} - \ln(Z) \\ t_{21} & t_{22} & \vdots & t_{2S} - \ln(Z) \\ \vdots & \vdots & \vdots & \vdots \\ t_{T1} & t_{T2} & \ldots & t_{TS} - \ln(Z) \end{bmatrix} - \ln(Z)$$

which has $T + 1$ unknowns (the T values of λ plus $\ln(Z)$) and S equations. The intercept is $\ln(Z)$ and each λ-value measures the degree to which the $\ln(\hat{p}_j)$ changes as the value of the trait changes, holding other traits constant.

Comparing the relative importance of traits When traits are standardised to unit variance, these λ-values can be directly compared to estimate the relative importance of different traits in determining community structure (Sonnier et al., 2010a). A positive λ-value for a given trait indicates that when other traits are held constant, species with greater values for this trait are more abundant in the local community than could be expected from the regional abundances, while negative λ-values indicate the opposite. A λ-

value of zero suggests that no selective force is exerted on this trait. Hence, provided that the predicted relative abundances obtained from the maxent model match well the observed ones, λ-values can provide information about the direction and strength of the selective force exerted on individuals with different traits during community assembly.

Eight continuous traits (height, LDMC, leaf area, LCC, LNC, LPC, LSC, and SLA), two ordinal traits (lifespan, acceptability to sheep) and one binary trait (ability to fix N) were used in the maxent models, for a total of 11 traits (Table 4.2). Prior to analysis, height, leaf area, LNC, LSC, LCC, and LPC were log-transformed to reduce the influence of species with large trait values, and all traits were then standardised to unit variance. When negative trait values were obtained from the log-transformation, $|x_{min}|$ was added to all values for that trait, where x_{min} is the minimum trait value. This translation was necessary for the Improved Iterative Scaling algorithm, which cannot accept negative values.

The maxent models were run on the 2007 vegetation cover data, which included all species (Table 4.1). In order to find a parsimonious set of traits and compare the selective advantage of different traits across all plots, a backward selection procedure was adopted, in which the trait with the smallest average absolute λ-value was progressively removed from the full set of traits, until only one trait remained in the model. To explore how excluding rare species affected the predictive capacity of the maxent model, models were also run with all 11 traits, but only for those species accounting for 99%, 90%, and 80% of the total abundance in each plot.

Using a more informative prior In an effort to increase predictive capacity of the full model including all species (Table 4.1), the backward selection procedure described above was repeated, but adding leaf thickness as a trait in the model, with and without a more informative "neutral" prior that took into account regional abundances of species. While acknowledging that dispersal itself is not necessarily a neutral process (Clark, 2009), this prior is referred to as "neutral" because it assumes (i) equal per capita probabilities of dispersal from the regional species pool to the local community, and (ii) equal per capita probabilities of survival and reproduction within the local

community. On the other hand, it is not truly neutral in that it does not necessarily assume equal per capita probabilities of survival and reproduction in the larger landscape (Shipley, 2010b). Adding such a neutral prior in maxent models can be done by summing the abundances of each species over all sites (Sonnier et al., 2010b; Shipley, 2010b). However, in this case the use of a neutral prior computed by summing the abundances of each species was not logical because many of the species had been sown at the beginning of the experiment, while others had colonized naturally. To take this into account, the regional species pool was split into sown (Table 4.1) and natural colonist species, and each set was given a total relative abundance of 0.5. This was justified by the fact that over-sowing with the rotary drill in 1982 led to about a third of the area disturbed and effectively sown, left a third relatively undisturbed (which still supported the initial vegetation), and left a further third disturbed and not sown (D. Scott, personal observation). Initial relative abundances of sown species were set proportional to their respective sowing rates on a weight basis (kg ha^{-1}); this makes the simplifying assumption that propagule pressure is best represented by total seed weight, and not seed number. Initial relative abundances of natural colonists were set proportional to their total relative abundances over the zero-fertiliser plots and the two controls, which represent the best-available estimates of the initial vegetation composition. When a species was not found in these plots, it was simply assigned the lowest prior probability.

Model validation and comparison of λ-values The fit between predicted and observed relative abundances was assessed through Pearson r^2. In addition, tests exploring whether the constraints in each maxent model significantly increased predictive capacity beyond the information already contained in the prior $\mathbf{q}$ were performed using the permutation tests recently described by Shipley (2010c). Although 999 permutations were specified for all tests, due to its computer-intensive nature the algorithm was stopped whenever the 95% confidence interval of the P-value did not include the α-level of 0.05 (Shipley, 2010c). All maxent models and permutation tests were done using the `maxent` and `maxent.test` functions, which are available as part of the `FD` package for R (Laliberté and Shipley, 2010).

Finally, the λ-values for each trait obtained from the maxent model including leaf thickness and an informative prior (i.e., the model that had the highest predictive capacity) were compared through ANOVA. Significant differences identified by ANOVA were further analysed using *post hoc* Tukey HSD tests. Doing so allows one to assess the selective advantage of different traits across the different experimental treatments.

Species Richness

Differences in plant species richness between fertiliser and grazing intensity treatments were tested using ANOVA and *post hoc* Tukey HSD tests. This was done for: (i) total species richness; (ii) native species richness; and (iii) exotic species richness. The 2007 vegetation cover data (i.e., year 26 of the experiment) were used for these analyses.

Null Models of Community Assembly and Trait Dispersion

Functional diversity metrics To explore whether the experimental treatments of soil resource addition (i.e., fertilisation and irrigation) and grazing intensity led to trait under- or over-dispersion (Weiher and Keddy, 1995), three different functional diversity metrics were measured in each plot, and the observed metrics were compared to those expected under a null model of community assembly. First, functional richness (FRic; Cornwell et al., 2006; Villéger et al., 2008) is the volume of the minimum convex hull that includes all species in multidimensional trait space. FRic is the multivariate analogue of the range and has been previously used to assess the importance of environmental filtering during community assembly (Cornwell et al., 2006). Second, functional evenness (FEve; Villéger et al., 2008) represents the regularity in the distribution of abundance in multidimensional trait space, and is the multivariate extension of the functional regularity index of Mouillot et al. (2005). An even spacing of species abundances in trait space is often interpreted as a signal that competitive interactions resulting in limiting similarity (MacArthur and Levins, 1967) were important during community assembly (Ricklefs and Travis, 1980; Weiher et al., 1998; Stubbs and Wilson, 2004; Mason et al., 2007; Ingram and Shurin, 2009).

Because FRic (and the range) is strongly influenced by species with extreme trait values (Cornwell et al., 2006), and because it cannot integrate information on species abundances, a third functional diversity metric was used, functional dispersion (FDis; see Chapter 2). FDis is the weighted average distance of individual species to the centroid of all species within a community, where weights are species relative abundances, and is the multivariate analogue of the weighted mean absolute deviation (Chapter 2). While FRic and FEve are by construction independent from each other (Villéger et al., 2008), simulations have shown that FDis is moderately positively correlated with FRic, and minimally with FEve (Chapter 2). FDis is conceptually and mathematically similar to Rao's quadratic entropy (Botta-Dukát, 2005, see also Chapter 2).

Using individual or multiple traits Trait over- or under-dispersion can be explored either in multidimensional space or using individual traits (Weiher et al., 1998). There are advantages and drawbacks to both approaches. On the one hand, using more than one trait (e.g., Weiher et al., 1998; Stubbs and Wilson, 2004) takes into account correlations between traits, but it can then be difficult to attribute the overall observed patterns to any particular trait. On the other hand, analysing individual traits (e.g., Kraft et al., 2008; Cornwell and Ackerly, 2009) can simplify interpretation, but does not consider correlations between traits and can increase the susceptibility to Type-I error due to multiple testing.

A three-step approach that combined both approaches was used. First, all traits (Table 4.2) were used, except leaf thickness (for reasons discussed on page 62), to measure the functional diversity metrics in multidimensional trait space (Chapter 2). Because traits were continuous, ordinal, or binary, and because some missing values were present (Table 4.2), a Gower dissimilarity matrix between species was used (Podani, 1999). In this second analysis, only the two continuous traits that best represented the two strongest independent axes of functional variation in the principal component analysis (i.e., the two traits that had the greatest loadings on the first two principal components) were selected. Because the two traits selected (LNC and height) were continuous, a Euclidean distance matrix was used to compute the functional

diversity metrics (Chapter 2). Third, all continuous traits were considered individually, except seed mass and onset of flowering for which missing values were present for some relatively abundant species (Table 4.2). For these univariate analyses, FRic was computed as the range (Kraft et al., 2008; Cornwell and Ackerly, 2009; Ingram and Shurin, 2009). All functional diversity metrics were computed using the `FD` package (Laliberté and Shipley, 2010).

Comparison to null expectations The observed functional diversity metrics were compared to those obtained from a null model of random community assembly. In contrast to other studies that used only presence-absence data in their null models (e.g., Weiher et al., 1998; Cornwell and Ackerly, 2009; Ingram and Shurin, 2009), this null model approach integrated species abundances. In order to convert the continuous abundance data to the count data required by the null model algorithm, all non-zero values in the abundance matrix were divided by the minimum non-zero value, and results were rounded to the nearest integer. To prevent regionally rare species from becoming abundant, and to avoid changes in species richness from influencing the null functional diversity metrics, the randomisation procedure was constrained such that species abundances across all plots (i.e., column marginals), as well as species richness per plot (i.e., number of structural zeros per row), were kept constant. A total of 999 null abundance matrices were generated using the '3x' algorithm of Hardy (2008), available as part of the `vegan` package (Oksanen et al., 2010).

To test for over- or under-dispersion within each plot, the number of times that the observed functional diversity metric in each plot was smaller, equal, or greater than the functional diversity metrics obtained from the null model was recorded. Because the test was two-tailed with $\alpha = 0.05$, statistically significant over-dispersion meant that only 2.5% of the null functional diversity values were equal or greater than the observed functional diversity metric, whereas under-dispersion meant that 2.5% of the null values were equal or smaller than the observed functional diversity metric. However, since such individual-plot measures of trait dispersion are stringent and can thus have lower power to detect non-random patterns (Stubbs and Wilson,

2004; Ingram and Shurin, 2009), the standardised deviations from the null expectation (z-scores) for each plot were also computed:

$$z = \frac{x - \mu_{null}}{\sigma_{null}}$$

where x is the observed functional diversity, μ_{null} is the mean of the null distribution, and σ_{null} is its standard deviation. To ensure that the z-scores were meaningful, they were only calculated when null distributions were approximately symmetric. The z-scores were compared among treatments, using ANOVA and *post hoc* Tukey HSD tests. Positive z-scores indicate a trend towards over-dispersion, while negative z-scores indicate a trend towards under-dispersion (Ingram and Shurin, 2009). All trait dispersion analyses were conducted on the 2007 vegetation cover data.

4.4 Results

4.4.1 Relationships among Species Traits

There were moderately strong ($|r| \geq 0.6$) and significant ($P \leq 0.05$) correlations between several of the functional traits measured (Fig. 4.1). A principal component analysis conducted on all continuous traits other than seed mass and onset of flowering (because of missing values for these two traits; Table 4.2) highlighted the inter-correlation between several traits along the two first principal components (Fig. 4.2a). Together, the first two principal components represented 74% of the variance in these traits. LNC, LPC, LSC, LDMC, and SLA all had strong loadings on the first axis, which explained 54.3% of the variance in traits (Fig. 4.2a). The second axis, which explained an additional 19.7% of the variance in traits, was primarily driven by height and LCC (Fig. 4.2a), although these two traits were not significantly correlated with each other (Fig. 4.1). LCC had the strongest loading on the third axis, which explained 9.9% of the variance in traits. There was a very sharp distinction between native and exotic species along the first principal component, with native species having distinctly greater than average LDMC values, and lower than average LNC, LSC, SLA, LSC, and LPC values than exotic species (Fig. 4.2a).

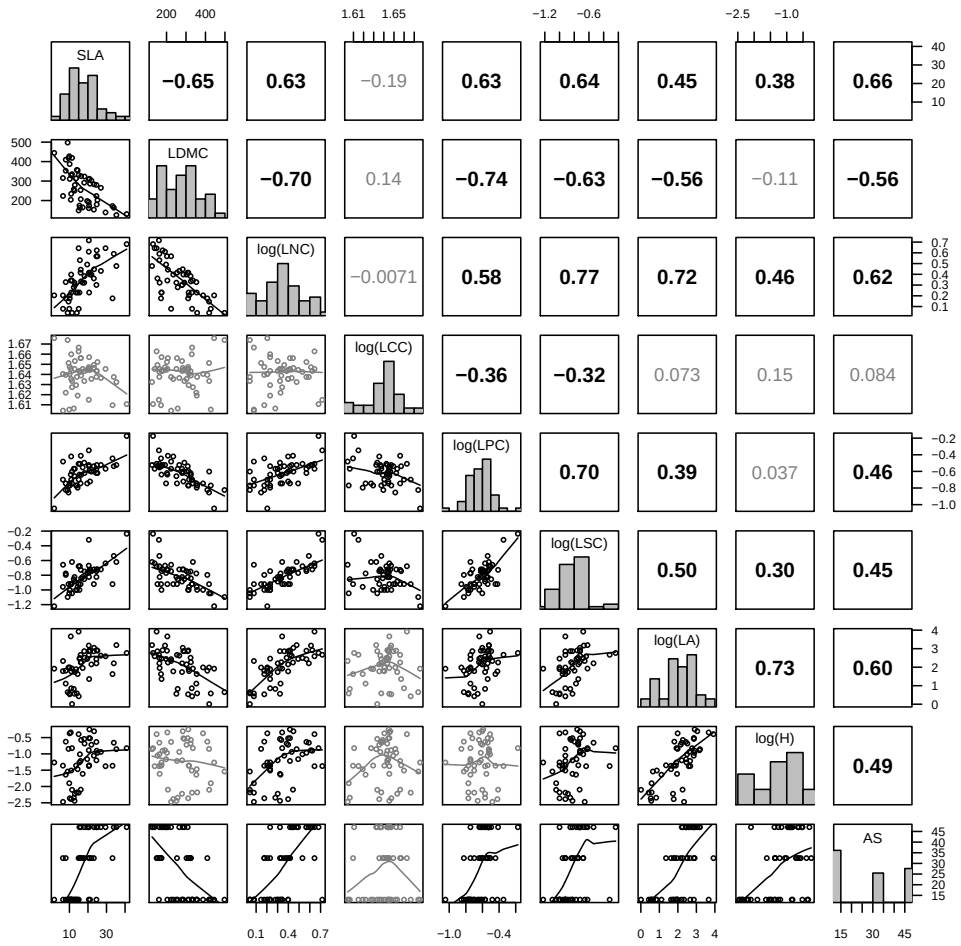

Figure 4.1: Scatterplot matrix showing the pairwise relationships among eight continuous and one ordinal (acceptability to sheep) traits for all species. The diagonal shows frequency histograms of individual traits. The lower left of diagonal shows individual scatterplots between pairs of traits. Smoothed loess curves (black lines; span = 0.9) were added to plots. The upper right of diagonal shows the Pearson correlation (r) coefficients. Values in black, bold characters indicate statistical significance at $\alpha = 0.05$, while values in small, grey characters indicate non-significant correlations; the same color rule applies to scatterplots in the lower diagonal. See Table 4.2 for a description of the trait codings.

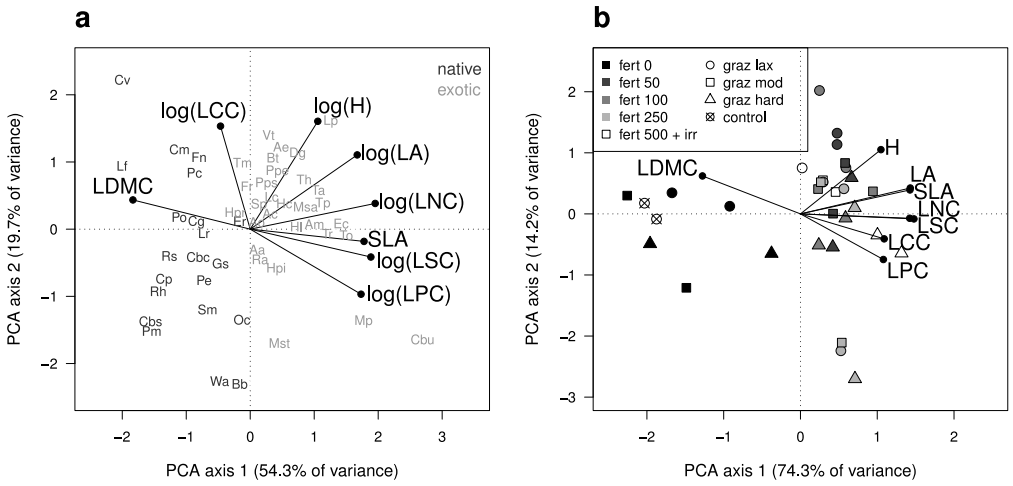

Figure 4.2: Principal component analysis correlation biplots (type-II scaling) showing the relationships among (**a**) nine traits (black vectors) for all species and (**b**) the same nine community-weighted traits (black vectors) for all 32 plots. Grey dots represent species. Traits that were log-transformed in (**a**) were also log-transformed in (**b**) before computing the community-weighted traits. See Table 4.2 for a description of the trait codings.

4.4.2 Shifts in Community-Weighted Traits

Temporal trends: fertiliser and Irrigation

0–5 year adjustment period In the 0–5 year adjustment period there were rapid changes in several community-weighted traits, such that distinct peaks (positive or negative) were often observed (Fig. 4.3). SLA_{cw} initially increased rapidly at all fertiliser levels, but became highest (≈ 26 m^2 kg^{-1}) in the high fertiliser/irrigated treatment (those receiving 500 kg ha^{-1} yr^{-1} of superphosphate), intermediate in the dryland fertilised treatments (≈ 20 m^2 kg^{-1}), and lowest in zero-fertiliser treatment (≈ 16 m^2 kg^{-1}). A similar trend was observed for AS_{cw}, although differences between the zero-fertiliser treatment and the dryland fertilised treatments were not clear. LT_{cw} decreased in the high fertiliser/irrigated treatment (≈ 0.20 mm) but increased in all other treatments (≈ 0.35 mm). LNC_{cw} and LSC_{cw} initially increased in all treatments, but more so in fertilised than in non-fertilised ones; $LDMC_{cw}$ showed a weak trend in the opposite direction, although there was little evidence for

differences between treatments. The trends in LNC_{cw} and LSC_{cw} matched the proportional increases in N-fixing species (NF_{cw}) among the different fertiliser treatments. LPC_{cw} showed a different pattern in that it initially increased to a greater level in zero-fertiliser than in fertilised treatments. LCC_{cw} increased in all treatments, but less so in high fertiliser/irrigated ones. SM_{cw} and LA_{cw} strongly increased in dryland fertilised treatments, increased moderately in non-fertilised plots, and remained stable in the high fertiliser/irrigated treatment. H_{cw} increased in the dryland fertilised treatments but remained stable in high fertiliser/irrigated and zero-fertiliser treatments. OF_{cw} was delayed in high fertiliser/irrigated treatments but did not vary in the other treatments. LS_{cw} remained stable throughout the initial adjustment period.

The changes in community-weighted traits during the adjustment period reflected marked increases in the relative abundance of N-fixing species (Fig. 4.4). *Lupinus polyphyllus*, a tall legume ($\sim$ 40 cm; see Fig. 4.15), rapidly increased in relative abundance in all but the highest fertiliser treatments (Fig. 4.4). Clovers (*Trifolium* spp.; see Table 4.1) increased in abundance in all dryland fertiliser treatments and particularly so at the highest fertiliser level, where they became dominant (Fig. 4.4).

5–20 year middle period The community-weighted traits that showed a rapid initial increase (or decrease) in the initial adjustment period (SLA_{cw}, AS_{cw}, LNC_{cw}, LSC_{cw}, LPC_{cw}, $LDMC_{cw}$, LCC_{cw}) shifted back to a value closer to the estimated starting value during the 5–20 year period (Fig. 4.3). For example, after its initial peak SLA_{cw} decreased strongly in the high fertiliser treatment, while it remained stable (after a temporary decrease) in the dryland (i.e., non-irrigated) fertiliser treatments and progressively decreased in the zero-fertiliser treatment. Consequently, all fertilised treatments converged towards a similar SLA_{cw} ($\approx$ 20 m^2 kg^{-1}) around year 15, while SLA_{cw} in the zero-fertiliser treatment was still distinctly lower ($\approx$ 15 m^2 kg^{-1}). Similar trends were observed for AS_{cw}, LNC_{cw} and NF_{cw}. LSC_{cw} remained stable after its initial peak for all fertilised treatments, while it consistently decreased in the zero-fertiliser treatment. $LDMC_{cw}$ increased in all treatments, but more so in the zero-fertiliser treatment, which had the highest

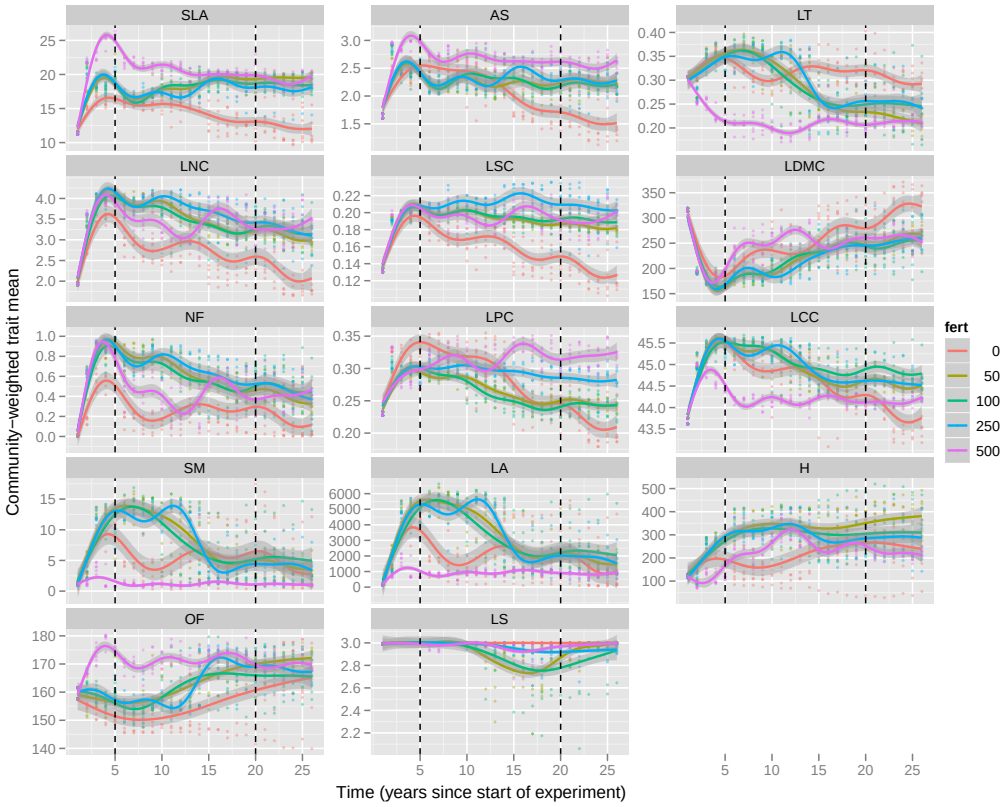

Figure 4.3: Shifts in community-weighted trait means among fertiliser treatments for the 27 years of the experiment (1981–2008). See Table 4.2 for units. Smoothed lines are fitted values from generalised additive models, with grey shaded areas representing standard errors. The vertical dashed lines correspond to the different periods.

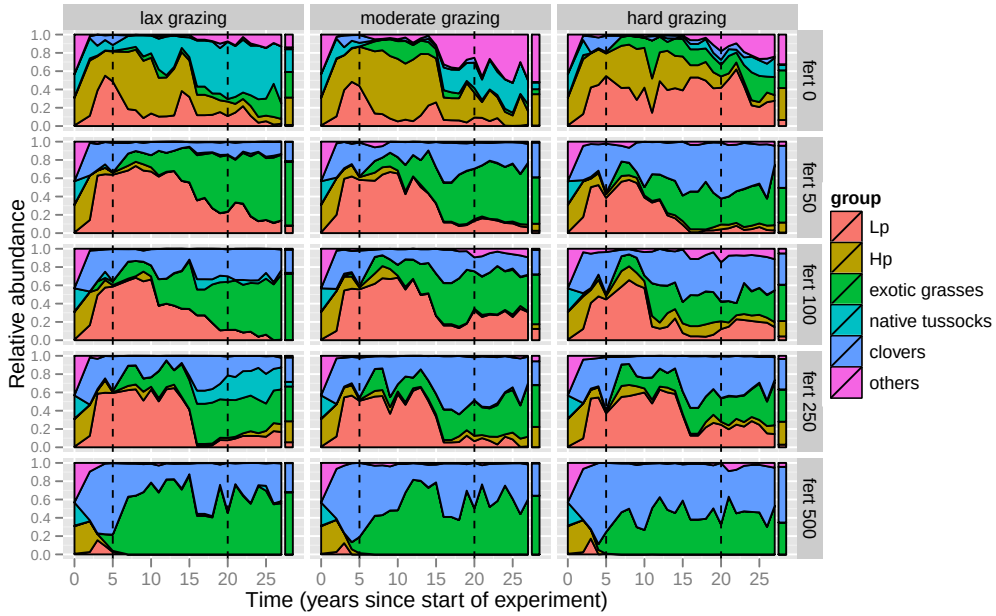

Figure 4.4: Relative abundance of particular species and groups of species for the 27 years of the experiment (1981–2008). See Table 4.1 for species codes. Exotic grasses include all exotic *Poaceae*. Native tussocks include *F. novae-zelandiae* and *Poa colensoi*. Clovers include all *Trifolium* spp. The vertical dashed lines correspond to the different periods. The detached columns on the far right side show the relative abundance of the different groups from the 2007 cover data (year 26).

$LDMC_{cw}$ at year 20. SM_{cw} and LA_{cw} (and to a lesser extent LT_{cw}) remained stable in the high fertiliser/irrigated treatment but decreased sharply in dryland fertilised treatments around year 15. OF_{cw} remained stable in the high fertiliser/irrigated treatment and increased progressively in all other treatments. H_{cw} remained relatively stable (showing only a slight increase) among treatments during the 5–20 year period. Throughout the middle period, a number dryland fertilised plots showed lower LS_{cw}, particularly in those receiving 50 and 100 kg ha^{-1} yr^{-1} of fertiliser. This period was marked by decreases in the abundance of *L. polyphyllus* in zero-fertiliser and dryland fertilised treatments, and increases in exotic grasses in all treatments (Fig. 4.4).

20–27 year post-fertiliser period The final post-fertiliser 20–27-year period was characterised by less temporal variability within treatments for most community-weighted traits. The main exception to this general trend was in the zero-fertiliser treatment, where SLA_{cw}, LNC_{cw}, LSC_{cw}, LPC_{cw}, and NF_{cw} steadily decreased, while $LDMC_{cw}$ kept increasing (Fig. 4.3). Similarly, there were smaller fluctuations in the relative abundance of different groups of species than in the previous two periods (Fig. 4.4).

Temporal Trends: Grazing Intensity

In contrast to the large differences that were observed among fertiliser treatments in the temporal trends of community-weighted traits, the differences among grazing intensity treatments were much subtler, and all three levels followed similar trajectories (Fig. 4.5). In general, differences among treatments became more apparent with time (particularly after around year 15), but such differences were always small and only noticeable for a few traits (e.g., AS_{cw}, LNC_{cw}, LSC_{cw}, $LDMC_{cw}$, NF_{cw}, and H_{cw}). Most notably, there was a trend for H_{cw} to increase under lower grazing intensity compared to the other two levels (Fig. 4.5).

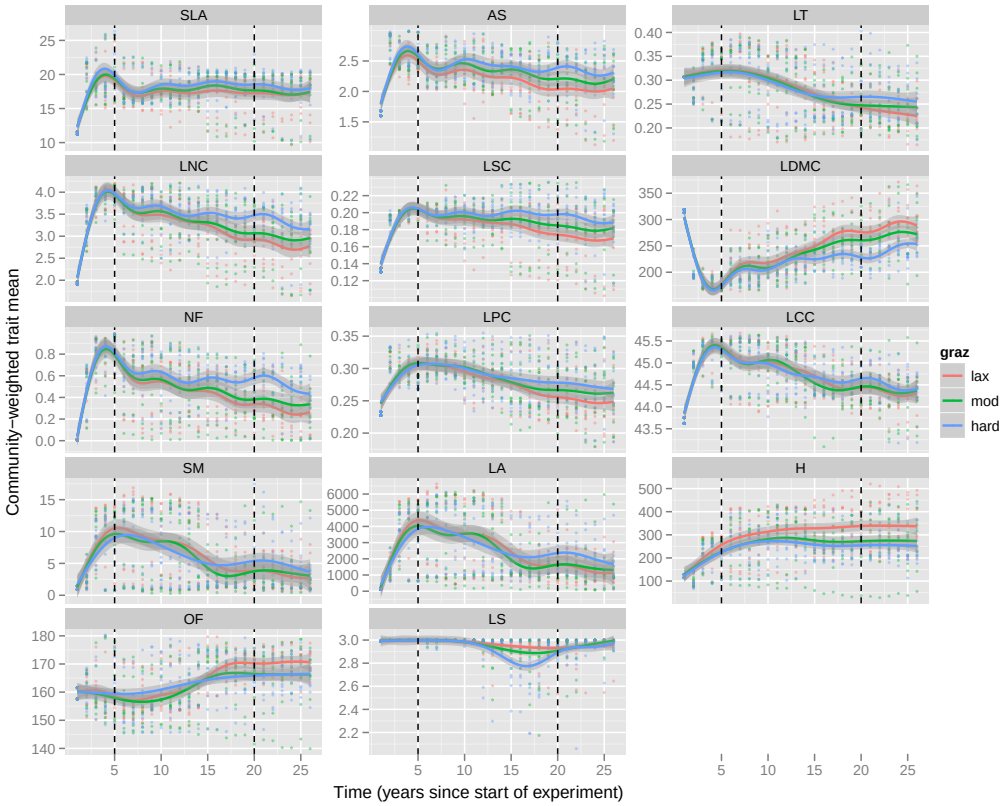

Figure 4.5: Shifts in community-weighted trait means among grazing intensity treatments for the 27 years of the experiment (1981–2008). See Table 4.2 for units. Smoothed lines are fitted values from generalised additive models, with grey shaded areas representing standard errors. The vertical dashed lines correspond to the different periods.

Differences in Community-Weighted Traits at Year 26

The pattern of trait variation observed at the species level (Fig. 4.2a) was also reflected at the community (plot) level (Fig. 4.2b). Though qualitatively similar, correlations between community-weighted traits were generally stronger than between species-level traits (Fig. 4.6).

A principal component analysis of community-weighted traits showed that plots receiving no fertiliser, as well as the two control plots, had greater than average $LDMC_{cw}$, and lower than average SLA_{cw}, LNC_{cw}, LSC_{cw}, and LPC_{cw}, than all fertilised plots (Fig. 4.2b). There was also a tendency for plots under low grazing to have greater H_{cw} than plots under moderate or high grazing (Fig. 4.2b).

There were significant ($P \leq 0.05$) differences between zero-fertiliser and fertilised treatments for SLA_{cw}, LA_{cw}, LSC_{cw}, and LNC_{cw}, which were all greater in the fertilised treatments, yet there were no differences among the different fertilised treatments (Fig. 4.7a). LPC_{cw}, H_{cw}, $LDMC_{cw}$ and LCC_{cw} did not significantly differ among fertiliser treatments (Fig. 4.7a). LSC_{cw} increased with grazing intensity, and differed significantly among all grazing intensity levels (Fig. 4.7b). LNC_{cw} was significantly lower under lax grazing than under hard grazing (Fig. 4.7b). LPC_{cw} was significantly higher at the highest grazing intensity, while the opposite was true for $LDMC_{cw}$ (Fig. 4.7b). H_{cw} was higher in the lax-grazing treatment than in the other two treatments (Fig. 4.7b). Two traits (LSC_{cw} and LPC_{cw}) showed significant fertiliser $\times$ grazing interactions. LSC_{cw} of high fertiliser/irrigated plots was significantly greater under hard grazing than under lax or moderate grazing (Fig. 4.8). For LPC_{cw}, the significant interaction was due to significant differences of the high fertiliser/irrigated treatments between lax and hard grazing, and similarly for the 100 kg ha^{-1} yr^{-1} fertiliser treatment (Fig. 4.8).

4.4.3 Selective Advantage of Traits

Prediction of relative abundances Using all community-weighted traits except leaf thickness, seed mass, and onset of flowering (Table 4.2) with a maximally uninformative uniform prior, 66% of the variation ($P \leq 0.05$) in the observed species relative abundances of all 51 species from the regional

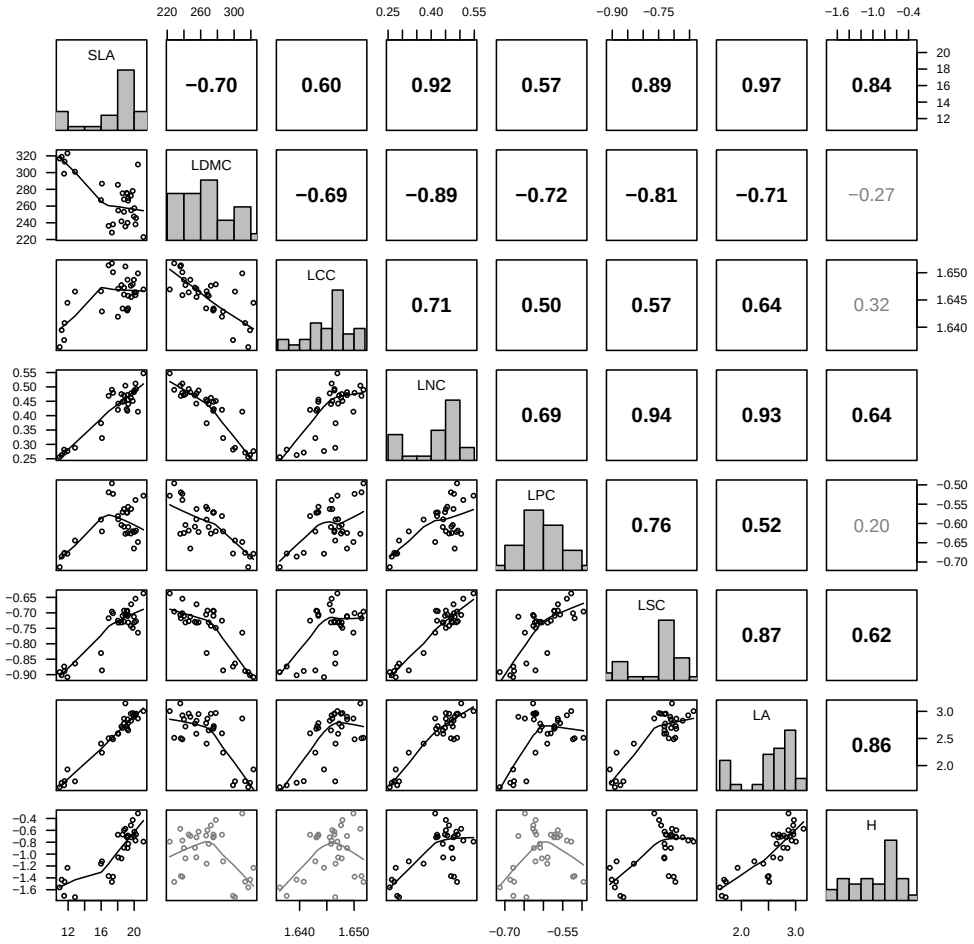

Figure 4.6: Scatterplot matrix showing the pairwise relationships among eight continuous community-weighted traits for all 32 plots, using the 2007 cover data. The diagonal shows frequency histograms of individual traits. The lower left of diagonal shows individual scatterplots between pairs of traits. Smoothed loess curves (black lines; span = 0.9) were added to plots. The upper right of diagonal shows the Pearson correlation (r) coefficients. Values in black, bold characters indicate statistical significance at $\alpha = 0.05$, while values in small, grey characters indicate non-significant correlations; the same color rule applies to scatterplots in the lower diagonal. See Table 4.2 for a description of the trait codings.

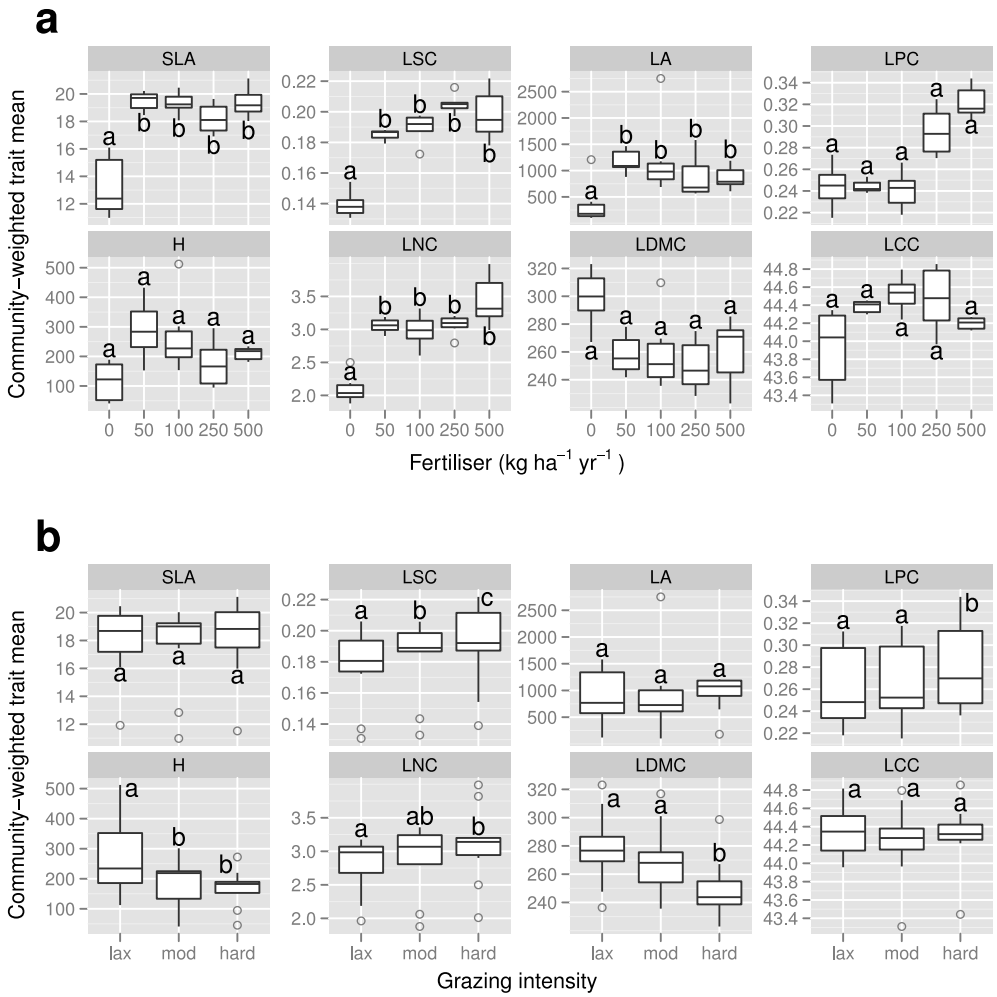

Figure 4.7: Boxplots showing the differences in community-weighted traits among (**a**) fertiliser and (**b**) grazing intensity treatments at year 26. Different letters indicate significant differences ($\alpha = 0.05$) based on *post hoc* Tukey HSD tests. The central bar shows the median, the box represents the interquartile range (IQR), the whiskers show the location of the most extreme data points still within 1.5 × IQR +/− the upper or lower quartiles, and the grey points are outliers. See Table 4.2 for a description of the trait codings and units. Statistical tests were based on community-weighted traits computed from log-transformed traits for H_{cw}, LCC_{cw}, LNC_{cw}, LPC_{cw}, LSC_{cw}, and LA_{cw}, but the figure shows untransformed community-weighted trait values. mod = moderate.

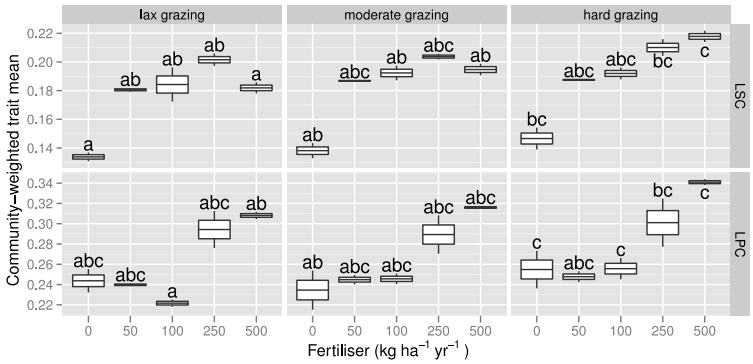

Figure 4.8: Boxplots showing the differences in community-weighted traits among fertiliser and grazing intensity treatments for two traits (LSC and LPC). For each trait (row), different letters indicate significant differences ($\alpha = 0.05$) based on *post hoc* Tukey HSD tests. See Table 4.2 for a description of the trait codings and units.

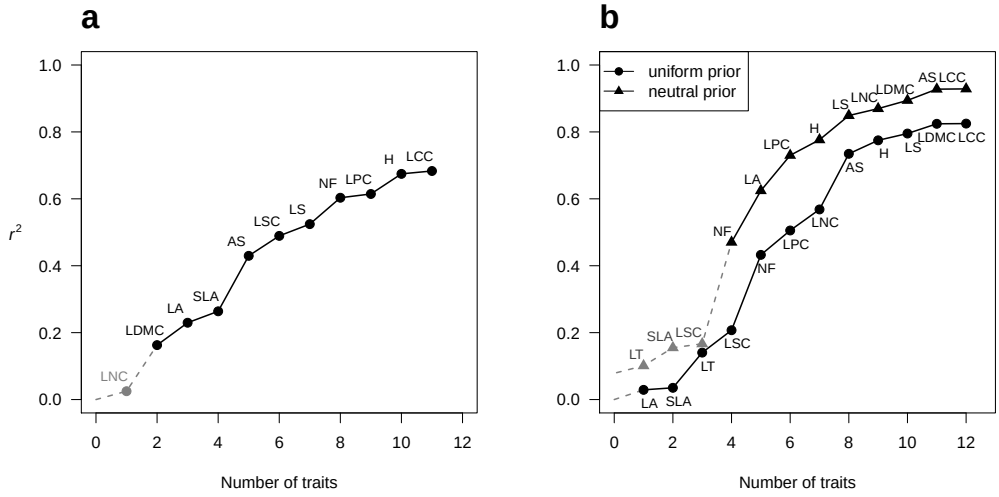

Figure 4.9: Predictive capacity (Pearson r^2) of the maxent model over all plots (including the two control plots) as the number of traits used increases. (**a**) All traits except leaf thickness (Table 4.2), uniform prior. (**b**) All traits including leaf thickness, using either a uniform or a more informative neutral prior. The black lines and trait labels show where the maxent models start becoming statistically significant ($P \leq 0.05$). See Table 4.2 for a description of the trait codings.

pool over the 32 plots was explained (Figs. 4.9a and 4.10a). Plotting the predicted against observed relative abundances on a logarithmic scale showed that rare species (those forming $< 5\%$ of total abundance per plot) were less well predicted than the most common ones (Fig. 4.10b). In this model, progressive removal of traits with the smallest absolute λ-values suggested that LNC, LDMC, leaf area and SLA were the most important traits, while LCC, height, LPC and ability to fix N were the least important ones (Fig. 4.9a). The predictive capacity of the maxent model was significant once two traits (LNC and LDMC) were included, although the resulting r^2 was low when only these two traits were considered (Fig. 4.9a).

Using a more informative neutral prior (details on page 69) in the model gave even better results ($r^2 = 0.784$, $P \leq 0.05$). Using the uniform prior but considering only the most-abundant species accounting for 99% (35 species in total), 90% (21 species), or 80% (16 species) of the total abundance in each plot yielded much better predictions (Fig. 4.11).

Compared with the initial model (Fig. 4.10a), adding leaf thickness as a trait in the maxent model greatly increased predictive capacity, particularly with the more informative prior ($r^2 = 0.929$, $P \leq 0.05$; Figs. 4.9b & 4.10c). In these new models leaf thickness, SLA, and LSC were important traits, while LDMC and LNC became much less important (Fig. 4.9b). In the model with the more informative prior, four traits (leaf thickness, SLA, LSC, and ability to fix N) were required to contribute significant predictive capacity beyond the information already contained in the prior. The model with the uniform prior attained significant predictive capacity when only one trait (leaf area) was added (Fig. 4.9b).

Comparison of λ-values For the maxent model with the highest predictive capacity (i.e., the one that included leaf thickness and a more informative neutral prior; Fig. 4.10c), species with greater leaf thickness were selected against at all fertiliser levels (i.e., negative λ-values) and there was a non-significant trend for this selection to become more negative under greater fertiliser application (Fig. 4.12a). A similar pattern was obtained for SLA, except that the trend was significant: SLA showed significantly stronger negative selection in the high fertiliser/irrigated treatment compared with the

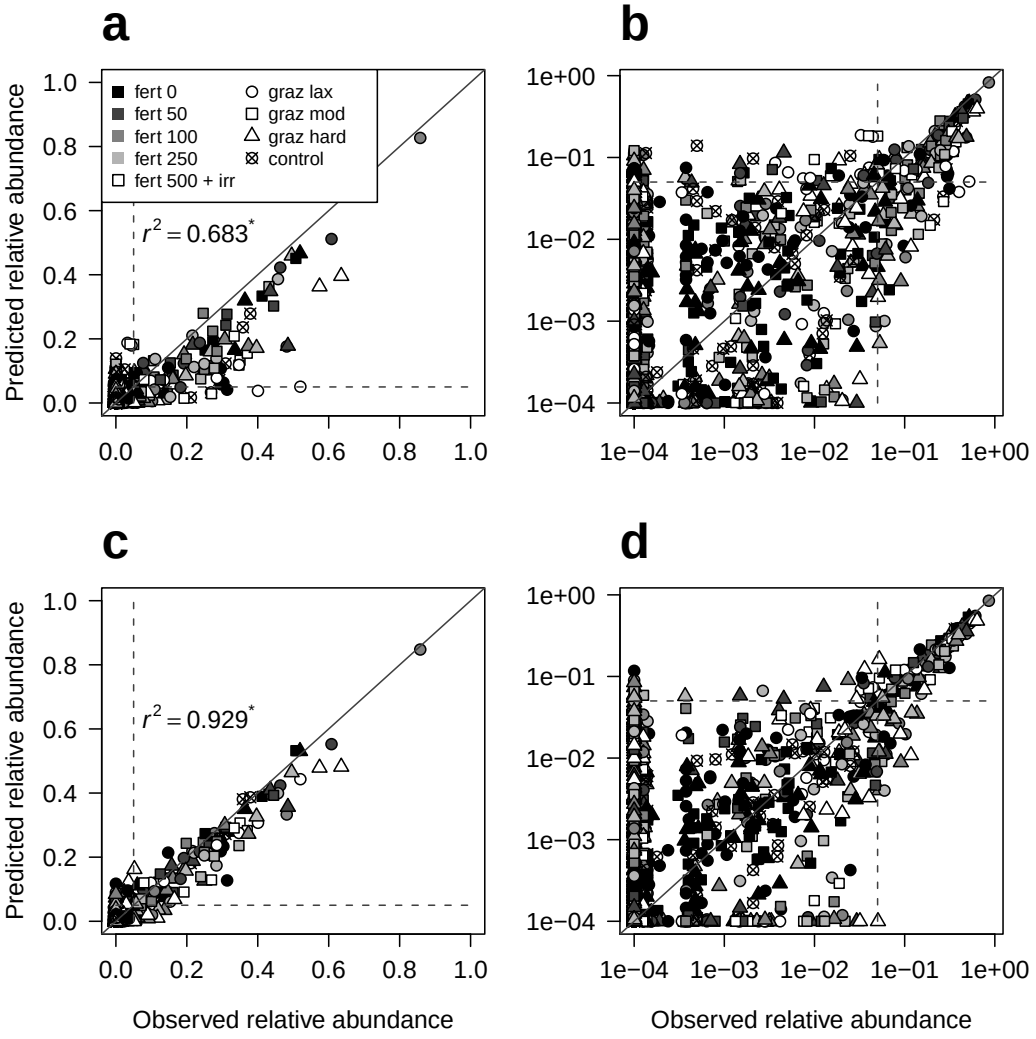

Figure 4.10: Results of maxent model for the 2007 vegetation cover data, using (**a**) all traits except leaf thickness and a uniform prior (see Fig. 4.9a) on arithmetic or (**b**) logarithmic scales (i.e., $\log_{10}(x) + 0.0001$), and using (**c**) all traits including leaf thickness with an informative neutral prior (see Fig. 4.9b) on arithmetic or (**d**) logarithmic scales. Analyses were done using all 32 plots and all species.$^*P \leq 0.05$. The dashed lines cut both axes at a relative abundance of 0.05 (5%).

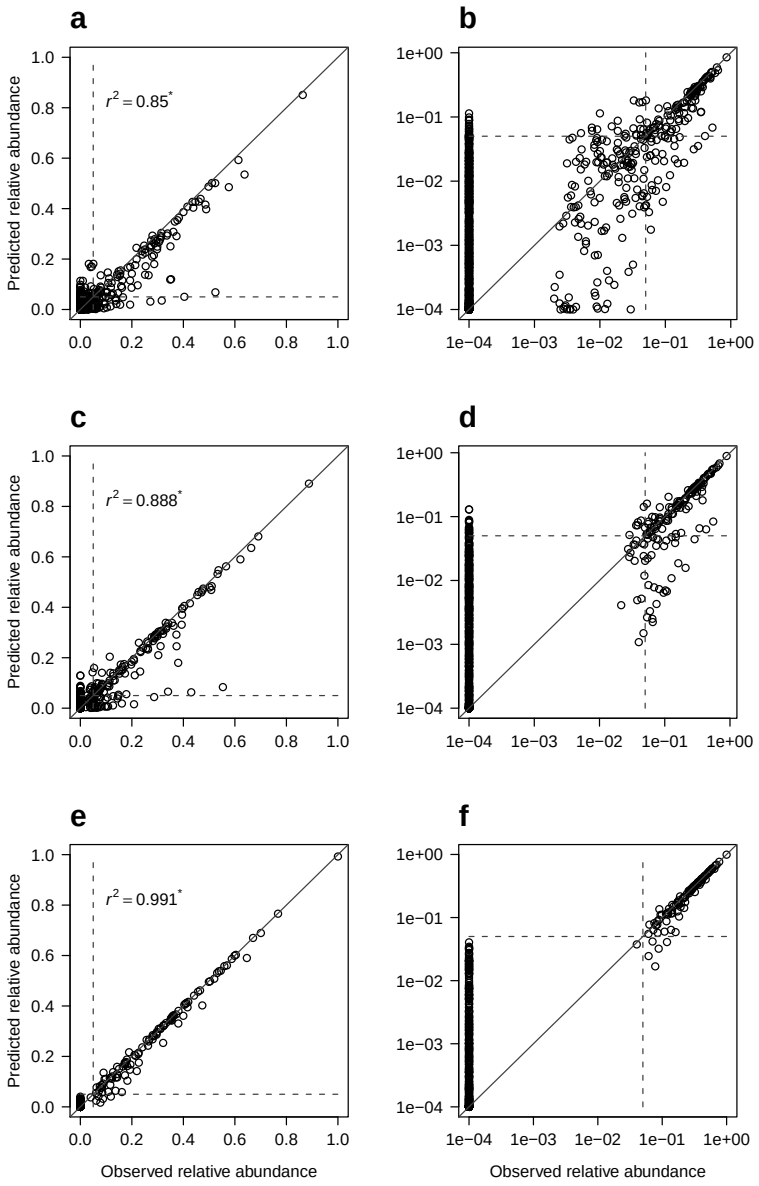

Figure 4.11: Results of maxent model for the 2007 vegetation cover data, using all traits (Table 4.2), but not at all species. (**a**–**b**) Only the 35 species corresponding to $\geq 99\%$ of total abundance in each plot; (**a**) arithmetic and (**b**) logarithmic (i.e., $\log_{10}(x) + 0.0001$) scales. (**c**–**d**) Same, but with only the 21 species corresponding to $\geq 90\%$ of total abundance in each plot, or (**e**–**f**) the 16 species corresponding to $\geq 80\%$ of total abundance in each plot. All analyses were done using all 32 plots, with a maximally uninformative (i.e., uniform) prior. $^*P \leq 0.05$.

zero-fertiliser treatment (Fig. 4.12a). Species with greater LSC and with the ability to fix N were under positive selection at all fertiliser levels, although this selection was significantly greater in the fertilised treatments compared to the non-fertilised one (Fig. 4.12a). There was also a significant difference in selection pressure for LDMC between the 50 kg ha^{-1} yr^{-1} and 500 kg ha^{-1} yr^{-1} treatments (Fig. 4.12a); the selection on LDMC was positive in the 50 kg ha^{-1} yr^{-1} treatment level, whereas it was negative at the highest fertiliser level.

With regard to grazing intensity, species with greater leaf thickness were more strongly selected against under lax grazing than under hard grazing (Fig. 4.12b). Significant differences in λ-values for height were also observed, such that species with greater height were positively selected for under lax grazing, but were selected against under moderate and hard grazing (Fig. 4.12b). LNC was under positive selection under lax grazing but selected against under hard grazing, and this difference was significant (Fig. 4.12b).

Significant fertiliser level $\times$ grazing intensity interactions on λ-values were detected for leaf thickness, SLA, and LNC (Fig. 4.13). In the 500 kg ha^{-1} yr^{-1} fertiliser treatment, both leaf thickness and SLA were under significantly greater negative selection under lax grazing than under hard grazing. At the same fertiliser level, LNC was under positive selection under lax grazing, yet was under negative selection under hard grazing.

4.4.4 Species Richness

There was no significant fertiliser level $\times$ grazing intensity interaction ($P = 0.38$) on total plant species richness at year 26 (i.e., in 2007). However, total species richness was significantly greater ($P \leq 0.05$) in non-fertilised than in fertilised plots, the latter containing only about half the number of species of the former (16 vs 29 species, respectively; Fig. 4.14a). Still, there was no significant difference in total species richness among the different fertilised treatments (Fig. 4.14a). Moreover, the number of exotic species did not vary among all fertiliser levels ($P = 0.583$); instead, differences in total species richness between non-fertilised and fertilised plots were due to the disproportionate loss of native species with fertilisation (Fig. 4.14a).

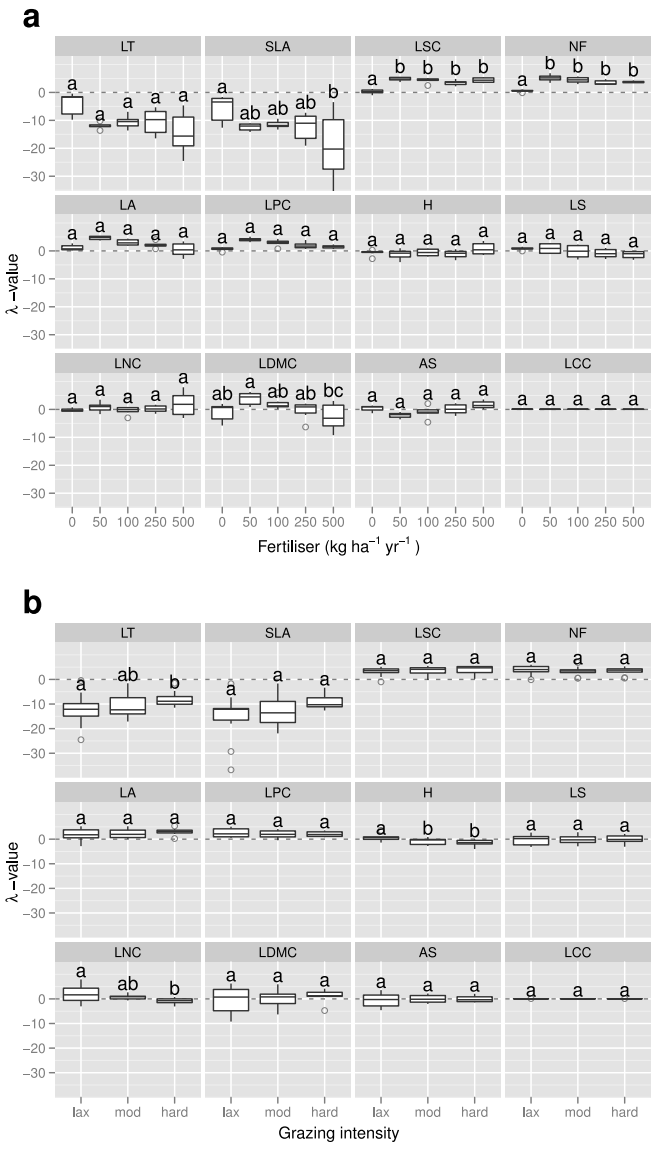

Figure 4.12: Boxplots showing the differences in λ-values among (**a**) fertiliser and (**b**) grazing intensity treatments for the 12 traits (including leaf thickness) used in the maxent model with the informative neutral prior (Fig 4.10c). Different letters indicate significant differences ($\alpha = 0.05$) based on *post hoc* Tukey HSD tests. Traits are ordered according to their importance, based on Fig. 4.9b. See Table 4.2 for a description of the trait codings.

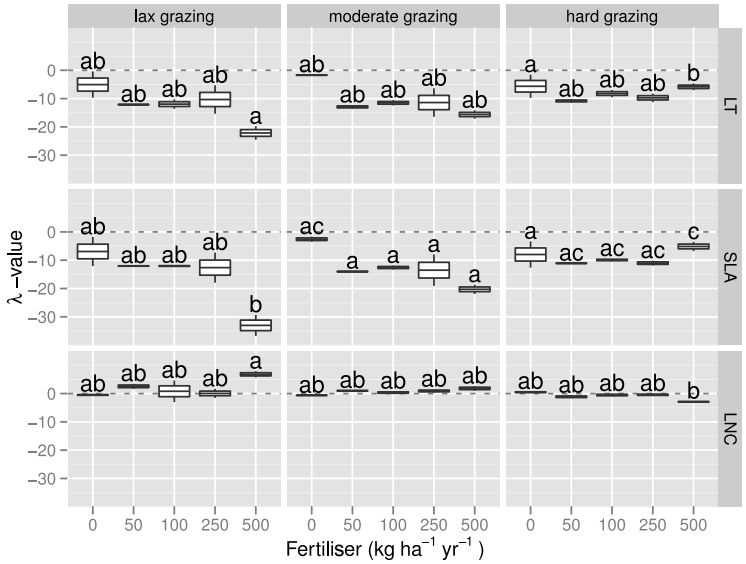

Figure 4.13: Boxplots showing the differences in λ-values among fertiliser and grazing intensity treatments for three traits (leaf thickness, SLA, and LNC) based on the maxent model with the informative prior (Fig 4.10c). For each trait (row), different letters indicate significant differences ($\alpha = 0.05$) based on *post hoc* Tukey HSD tests. Traits are ordered according to their importance, based on Figure 4.9b. See Table 4.2 for a description of the trait codings.

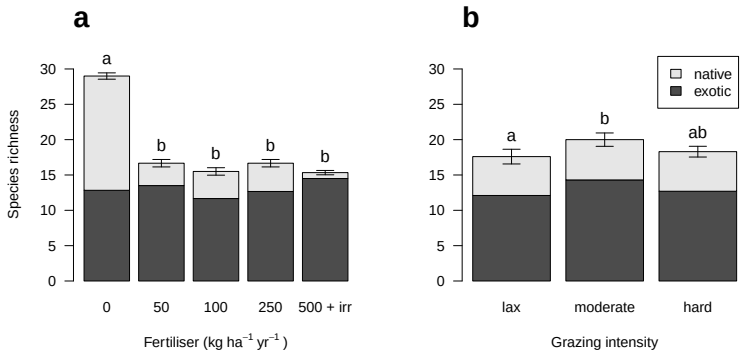

Figure 4.14: Plant species richness under different (**a**) fertiliser and (**b**) grazing intensity treatments (year 26; 2007 vegetation cover data). Richness is divided between native and exotic species. Different letters indicate significant ($P \leq 0.05$) differences in total species richness between treatments, following a *post hoc* Tukey HSD test.

Non-fertilised plots contained a significantly greater number of native species than all other fertiliser levels, and high fertiliser/irrigated plots (i.e., those receiving 500 kg ha^{-1} yr^{-1} of fertiliser) had significantly lower native species richness than the 100 or 250 kg ha^{-1} yr^{-1} treatments. Figure 4.15 shows the native and exotic species that were present under the different fertiliser treatments.

Both total and exotic species richness were significantly greater under moderate grazing than under lax grazing (Fig. 4.14b), whereas native species richness did not significantly differ among grazing intensity treatments. However, differences between grazing intensity levels (Fig. 4.14b) were much smaller than differences between fertiliser levels (Fig. 4.14a).

4.4.5 Trait Over- and Under-Dispersion

For several trait combinations as well as individual traits, high fertiliser/irrigated plots often showed significant under-dispersion of FRic ($P \leq 0.025$, because the main test was two-tailed; Table 4.3). For example, when all traits were considered together, five out of six of the high fertiliser/irrigated plots showed significant under-dispersion ($P \leq 0.025$), and the sixth plot still showed marginally significant under-dispersion ($P = 0.051$). Similar

		Functional richness (FRic)		Functional dispersion (FDis)		Functional evenness (FEve)	
Fertiliser	Traits	Obs $\ll$ Null	Obs $\gg$ Null	Obs $\ll$ Null	Obs $\gg$ Null	Obs $\ll$ Null	Obs $\gg$ Null
0	All	1/8					1/8
0	LNC + H						1/8
0	LNC						
0	H	1/8				1/8	
0	SLA						
0	LDMC				1/8		
0	LPC	1/6			6/8		
0	LSC				1/8		2/8
0	LCC				4/8		1/8
0	LA			1/6			
50	All						
50	LNC + H						
50	LNC						
50	H						
50	SLA			2/6			
50	LDMC						
50	LPC						
50	LSC						
50	LCC						
50	LA						
100	All			1/6			
100	LNC + H			1/6			
100	LNC			1/6			
100	H					1/6	
100	SLA			1/6			
100	LDMC			1/6			
100	LPC			1/6		1/6	
100	LSC			1/6		1/6	
100	LCC			1/6		1/6	
100	LA			1/6			
250	All						1/6
250	LNC + H						
250	LNC						
250	H					1/6	
250	SLA	1/6					
250	LDMC						
250	LPC						
250	LSC					1/6	
250	LCC					1/6	
250	LA						
500	All	5/6				1/6	
500	LNC + H	5/6					
500	LNC	1/6				1/6	
500	H	3/6		1/6			
500	SLA						1/6
500	LDMC	4/6					
500	LPC					1/6	
500	LSC						
500	LCC	2/6					
500	LA	6/6					1/6

Table 4.3: Number of plots where functional diversity was significantly lower or greater than the null expectation for each fertiliser level/trait(s) combination. The test of no difference in trait dispersion was two-tailed with $\alpha = 0.05$, such that statistically significant over-dispersion (Obs $\gg$ Null) means that only 2.5% of the null functional diversity values were equal or greater than the observed functional diversity metric, whereas under-dispersion (Obs $\ll$ Null) meant that 2.5% of the null values were equal or smaller than the observed functional diversity metric. Results are shown as fractions of the total number of plots, but only cases where at least one plot was significantly different from the null expectation are shown. The two control plots were added to the zero-fertiliser treatment, hence the total of eight plots for that level.

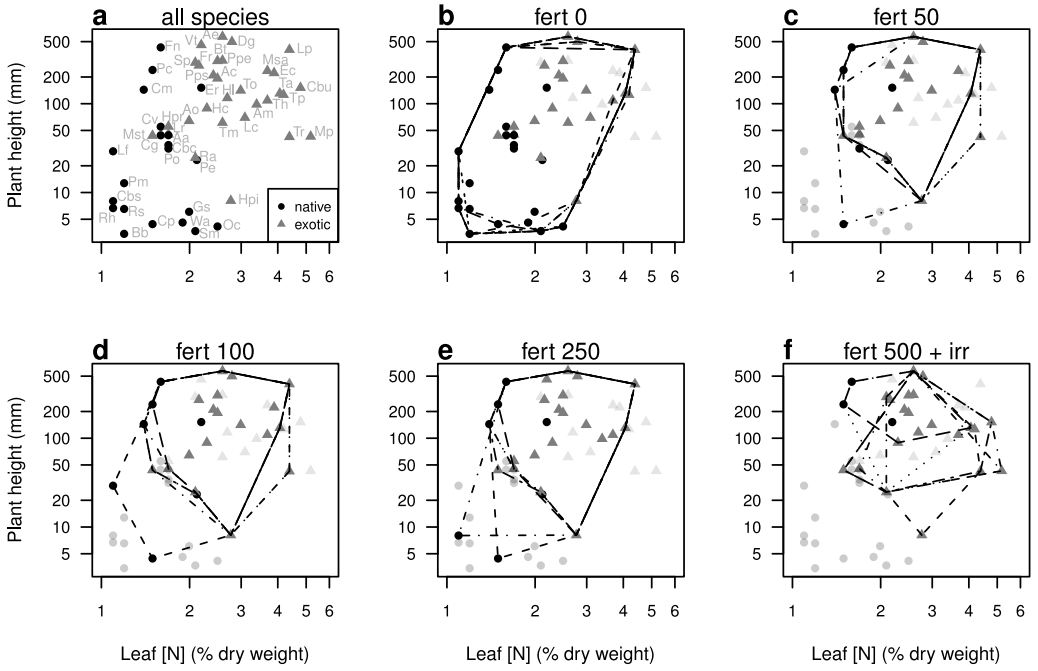

Figure 4.15: Reduced functional richness under increasing soil resource availability (fertiliser and irrigation). (**a**) All species plotted in a two-dimensional trait space defined by leaf [N] and plant height. Axes are on logarithmic scales. Panels **b**–**f** show, for each fertiliser level, the minimum convex hulls (polygons) that include all species within each site, a measure of functional richness. Each polygon (with different line types) represents an individual site. Black circles indicate native species, while grey triangles indicate exotic species. Darker symbols in panels **b**–**f** show the species that are present in at least one site, while lighter symbols indicate the species that are absent from all sites.

results were obtained when only LNC and height were considered together, and Figure 4.15 shows that these results were due to the complete loss of species with low height and/or lower LNC in high fertiliser/irrigated plots. For leaf area, all six plots of the highest fertiliser treatment showed significant under-dispersion (Table 4.3). Two other traits also showed fairly consistent under-dispersion in this same treatment: LDMC (four plots out of six) and LNC (three plots out of six; Table 4.3).

Second, the distribution of abundance along LPC and LCC axes in plots receiving no fertiliser was significantly more dispersed than expected (i.e.,

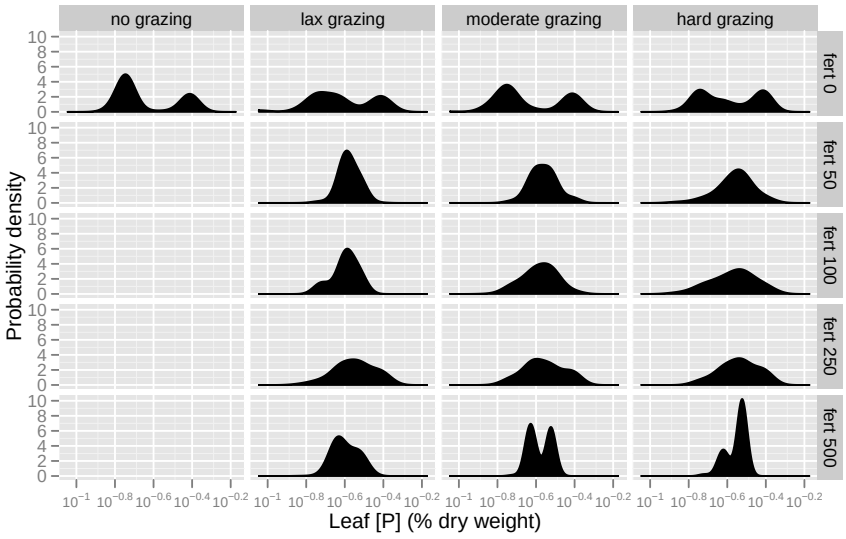

Figure 4.16: Abundance-weighted leaf phosphorous concentration (LPC) distributions across the experimental treatments. Each distribution is an average of two plots (replicates). The x-axis is on a logarithmic scale.

significantly greater FDis; Table 4.3). Indeed, six out of eight zero-fertiliser plots (including the two control plots) had significantly greater than expected FDis for LPC, whereas four out of eight plots showed this pattern for LCC (Table 4.3). For LPC and LCC, such over-dispersion could clearly be seen from the abundance-weighted distributions, which showed a greater spread in the unfertilised treatment (Figs. 4.16 and 4.17).

Deviations from Null Expectations

With the exception of the strongly right-skewed null distributions of FRic values obtained when all traits were considered simultaneously, null distributions of functional diversity metrics per plot were reasonably symmetric, thus enabling us to compare standardised deviations from the null expectations (i.e., z-scores) among the different experimental treatments (Tables 4.4, 4.5).

For FRic, there was a significantly greater trend towards under-dispersion (i.e., significantly smaller, negative standardised deviation from the null expectation) in high fertiliser/irrigated plots compared to the other fertiliser treatments when LNC and height were considered simultaneously (Table 4.4;

		Fertiliser level				
Metric	Traits	0	50	100	250	500
FRic	All*	-	-	-	-	-
	LNC + H	$\mathbf{-0.27 \pm 0.23}^{a}$	$\mathbf{-0.75 \pm 0.32}^{a}$	$\mathbf{-0.32 \pm 0.38}^{a}$	$\mathbf{-0.74 \pm 0.32}^{a}$	$\mathbf{-2.56 \pm 0.23}^{b}$
	LNC	-0.25 ± 0.13^{a}	-1.06 ± 0.25^{a}	-0.37 ± 0.29^{a}	-0.55 ± 0.28^{a}	-1.21 ± 0.21^{a}
	H	-0.09 ± 0.49^{a}	-0.63 ± 0.31^{a}	-0.41 ± 0.24^{a}	-0.63 ± 0.31^{a}	-2.87 ± 0.58^{a}
	SLA	-0.01 ± 0.19^{a}	0.29 ± 0.14^{a}	0.02 ± 0.31^{a}	-1.08 ± 0.41^{a}	-0.02 ± 0.33^{a}
	LDMC	$\mathbf{0.40 \pm 0.16}^{a}$	$\mathbf{-0.34 \pm 0.20}^{ab}$	$\mathbf{0.09 \pm 0.42}^{a}$	$\mathbf{-0.49 \pm 0.07}^{ab}$	$\mathbf{-1.67 \pm 0.58}^{b}$
	LPC	0.19 ± 0.27^{a}	-0.18 ± 0.14^{a}	0.07 ± 0.08^{a}	-0.06 ± 0.07^{a}	-0.30 ± 0.58^{a}
	LSC	-0.44 ± 0.07^{a}	-0.44 ± 0.10^{a}	-0.25 ± 0.23^{a}	-0.46 ± 0.08^{a}	0.03 ± 0.19^{a}
	LCC	0.89 ± 0.06^{a}	0.00 ± 0.17^{a}	-0.37 ± 0.46^{a}	-1.31 ± 0.27^{a}	-1.24 ± 0.39^{a}
	LA	$\mathbf{0.56 \pm 0.37}^{a}$	$\mathbf{-0.76 \pm 0.32}^{b}$	$\mathbf{-0.40 \pm 0.23}^{ab}$	$\mathbf{-0.04 \pm 0.48}^{ab}$	$\mathbf{-2.73 \pm 0.10}^{c}$
FDis	All	0.03 ± 0.19^{a}	-0.24 ± 0.26^{a}	0.16 ± 0.74^{a}	-0.01 ± 0.26^{a}	-0.23 ± 0.13^{a}
	LNC + H	-0.07 ± 0.58^{a}	-0.52 ± 0.29^{a}	-0.60 ± 0.46^{a}	-0.01 ± 0.48^{a}	-0.90 ± 0.14^{a}
	LNC	-0.44 ± 0.26^{a}	0.21 ± 0.15^{a}	-0.06 ± 0.48^{a}	-0.09 ± 0.23^{a}	0.51 ± 0.14^{a}
	H	0.40 ± 0.43^{a}	-0.48 ± 0.19^{a}	-0.61 ± 0.22^{a}	-0.05 ± 0.55^{a}	-1.16 ± 0.07^{a}
	SLA	-0.00 ± 0.19^{a}	-1.08 ± 0.17^{a}	-0.75 ± 0.22^{a}	-0.59 ± 0.19^{a}	-0.61 ± 0.11^{a}
	LDMC	0.87 ± 0.23^{a}	0.21 ± 0.09^{a}	-0.23 ± 0.49^{a}	-0.10 ± 0.21^{a}	0.10 ± 0.11^{a}
	LPC	2.22 ± 0.34^{a}	-0.92 ± 0.25^{a}	-0.20 ± 0.47^{a}	-0.16 ± 0.49^{a}	-0.92 ± 0.17^{a}
	LSC	0.56 ± 0.55^{a}	-0.39 ± 0.08^{a}	-0.70 ± 0.19^{a}	-0.64 ± 0.15^{a}	0.18 ± 0.21^{a}
	LCC	$\mathbf{1.80 \pm 0.39}^{a}$	$\mathbf{-0.91 \pm 0.13}^{b}$	$\mathbf{-0.59 \pm 0.30}^{b}$	$\mathbf{-0.21 \pm 0.30}^{b}$	$\mathbf{-0.87 \pm 0.08}^{b}$
	LA	-0.45 ± 0.44^{a}	-0.89 ± 0.21^{a}	-0.66 ± 0.29^{a}	-0.25 ± 0.11^{a}	-0.53 ± 0.21^{a}
FEve	All	1.03 ± 0.40^{a}	-0.32 ± 0.32^{a}	-0.03 ± 0.33^{a}	0.12 ± 0.50^{a}	-0.75 ± 0.31^{a}
	LNC + H	$\mathbf{1.28 \pm 0.27}^{a}$	$\mathbf{-0.18 \pm 0.25}^{b}$	$\mathbf{-0.36 \pm 0.47}^{b}$	$\mathbf{-0.56 \pm 0.54}^{b}$	$\mathbf{-0.69 \pm 0.30}^{b}$
	LNC	$\mathbf{0.07 \pm 0.27}^{ab}$	$\mathbf{-0.54 \pm 0.24}^{ab}$	$\mathbf{0.39 \pm 0.37}^{a}$	$\mathbf{0.14 \pm 0.32}^{ab}$	$\mathbf{-0.91 \pm 0.20}^{b}$
	H	-0.17 ± 0.50^{a}	0.06 ± 0.28^{a}	0.00 ± 0.38^{a}	-0.19 ± 0.49^{a}	-0.41 ± 0.32^{a}
	SLA	0.44 ± 0.27^{a}	-0.23 ± 0.28^{a}	-0.52 ± 0.39^{a}	0.13 ± 0.37^{a}	0.49 ± 0.52^{a}
	LDMC	0.97 ± 0.13^{a}	-0.06 ± 0.38^{a}	0.12 ± 0.45^{a}	-0.29 ± 0.37^{a}	-0.16 ± 0.24^{a}
	LPC	0.76 ± 0.23^{a}	-0.63 ± 0.28^{a}	-0.23 ± 0.46^{a}	-0.10 ± 0.50^{a}	-0.90 ± 0.41^{a}
	LSC	1.40 ± 0.33^{a}	-0.58 ± 0.39^{a}	0.23 ± 0.43^{a}	-0.57 ± 0.36^{a}	-0.20 ± 0.38^{a}
	LCC	1.35 ± 0.34^{a}	-0.58 ± 0.33^{a}	0.06 ± 0.44^{a}	-0.02 ± 0.52^{a}	-0.29 ± 0.41^{a}
	LA	0.77 ± 0.11^{a}	-0.08 ± 0.36^{a}	-0.55 ± 0.33^{a}	0.02 ± 0.18^{a}	-0.07 ± 0.65^{a}

Table 4.4: Standardised deviations (means ± SE) from null expectations among fertiliser treatments for the different functional diversity metrics. For each functional diversity metric/trait(s) combination (i.e., for each row), different superscript letters indicate significant differences ($P \leq 0.05$) between fertiliser levels. *Not calculated because of strong skewness in the null distributions.

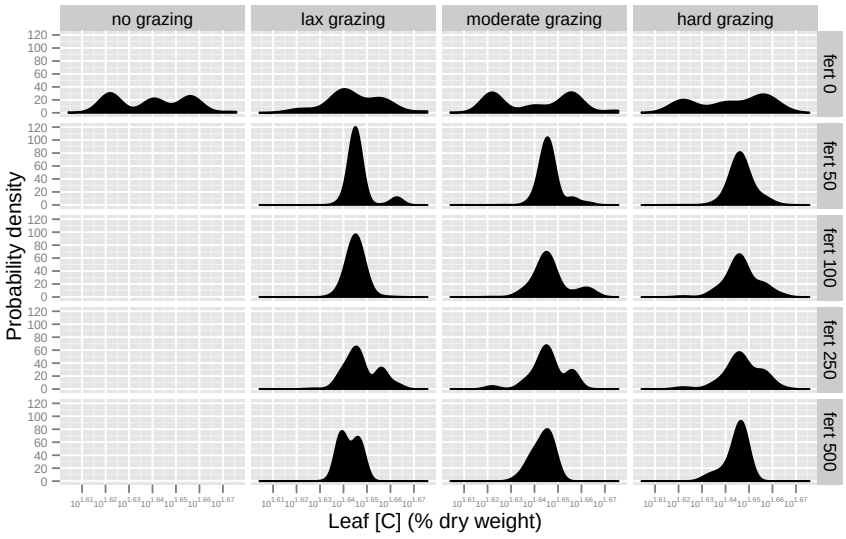

Figure 4.17: Abundance-weighted leaf carbon concentration (LCC) distributions across the experimental treatments. Each distribution is an average of two plots (replicates). The x-axis is on a logarithmic scale.

Fig. 4.15). These trends were also reflected by the mean deviations for LNC and height, although differences between fertiliser levels were not statistically significant when these two traits were considered individually. A significantly greater trend towards under-dispersion (i.e., reduced range) was found for LDMC in high fertiliser/irrigated plots compared to plots receiving 0 or 100 kg ha^{-1} yr^{-1} of fertiliser (Table 4.4). There was also a significant trend towards greater under-dispersion for leaf area in high fertiliser/irrigated plots compared to all other fertiliser treatments, and 50 kg ha^{-1} yr^{-1} plots compared to plots receiving no fertiliser (Table 4.4). With regard to grazing intensity, LCC showed a significantly greater trend towards under-dispersion under lax grazing than under hard grazing (Table 4.5).

For FDis, there was a significant difference in deviations between the zero-fertiliser vs fertilised treatments for LCC, with a trend towards over-dispersion under the zero-fertiliser but towards under-dispersion in the fertilised treatments (Table 4.4). This pattern could be detected from the LCC distributions (Fig. 4.17), which were more platikurtic in plots receiving no fertiliser than among the fertilised plots. There was also a significantly greater

		Grazing intensity		
Metric	Traits	lax	moderate	hard
FRic	All*	-	-	-
	LNC + H	-0.96 ± 0.237^{a}	-1.33 ± 0.19^{a}	-0.49 ± 0.41^{a}
	LNC	-0.84 ± 0.14^{a}	-0.91 ± 0.15^{a}	-0.31 ± 0.28^{a}
	H	-0.84 ± 0.52^{a}	-1.24 ± 0.36^{a}	-0.70 ± 0.43^{a}
	SLA	-0.10 ± 0.34^{a}	-0.17 ± 0.23^{a}	-0.20 ± 0.23^{a}
	LDMC	-0.22 ± 0.11^{a}	-0.74 ± 0.34^{a}	-0.24 ± 0.47^{a}
	LPC	-0.14 ± 0.20^{a}	-0.01 ± 0.26^{a}	-0.01 ± 0.21^{a}
	LSC	-0.39 ± 0.06^{a}	-0.15 ± 0.32^{a}	0.05 ± 0.31^{a}
	LCC	$\mathbf{-0.68 \pm 0.43}^{a}$	$\mathbf{-0.39 \pm 0.26}^{ab}$	$\mathbf{-0.15 \pm 0.34}^{b}$
	LA	-0.84 ± 0.34^{a}	-0.93 ± 0.45^{a}	-0.25 ± 0.50^{a}
FDis	All	-0.32 ± 0.40^{a}	-0.04 ± 0.21^{a}	0.17 ± 0.19^{a}
	LNC + H	-0.07 ± 0.58^{a}	-0.52 ± 0.29^{a}	-0.60 ± 0.46^{a}
	LNC	-0.09 ± 0.29^{a}	-0.06 ± 0.19^{a}	0.10 ± 0.20^{a}
	H	-0.25 ± 0.34^{a}	-0.61 ± 0.25^{a}	-0.23 ± 0.32^{a}
	SLA	-0.66 ± 0.17^{a}	-0.59 ± 0.20^{a}	-0.57 ± 0.16^{a}
	LDMC	-0.02 ± 0.30^{a}	0.32 ± 0.19^{a}	0.20 ± 0.18^{a}
	LPC	-0.23 ± 0.48^{a}	0.08 ± 0.51^{a}	0.15 ± 0.40^{a}
	LSC	0.05 ± 0.35^{a}	-0.26 ± 0.25^{a}	-0.37 ± 0.14^{a}
	LCC	-0.44 ± 0.27^{a}	0.02 ± 0.46^{a}	-0.04 ± 0.40^{a}
	LA	$\mathbf{-0.90 \pm 0.25}^{a}$	$\mathbf{-0.37 \pm 0.16}^{b}$	$\mathbf{-0.39 \pm 0.18}^{b}$
FEve	All	0.56 ± 0.38^{a}	-0.23 ± 0.25^{a}	-0.29 ± 0.31^{a}
	LNC + H	0.26 ± 0.39^{a}	-0.31 ± 0.37^{a}	-0.25 ± 0.31^{a}
	LNC	$\mathbf{0.35 \pm 0.32}^{a}$	$\mathbf{-0.44 \pm 0.17}^{b}$	$\mathbf{-0.41 \pm 0.20}^{b}$
	H	$\mathbf{-0.72 \pm 0.29}^{a}$	$\mathbf{0.10 \pm 0.29}^{ab}$	$\mathbf{0.20 \pm 0.22}^{b}$
	SLA	-0.26 ± 0.30^{a}	0.13 ± 0.24^{a}	0.30 ± 0.35^{a}
	LDMC	-0.04 ± 0.26^{a}	0.15 ± 0.30^{a}	0.24 ± 0.30^{a}
	LPC	0.06 ± 0.36^{a}	-0.37 ± 0.36^{a}	-0.35 ± 0.30^{a}
	LSC	0.05 ± 0.38^{a}	-0.03 ± 0.36^{a}	0.15 ± 0.38^{a}
	LCC	0.54 ± 0.43^{a}	-0.07 ± 0.33^{a}	-0.15 ± 0.31^{a}
	LA	0.02 ± 0.22^{a}	-0.24 ± 0.33^{a}	0.28 ± 0.36^{a}

Table 4.5: Standardised deviations (means ± SE) from null expectations among grazing intensity treatments for the different functional diversity metrics. For each functional diversity metric/trait(s) combination (i.e., for each row), different superscript letters indicate significant differences ($P \leq 0.05$) between fertiliser levels. *Not calculated because of strong skewness in the null distributions.

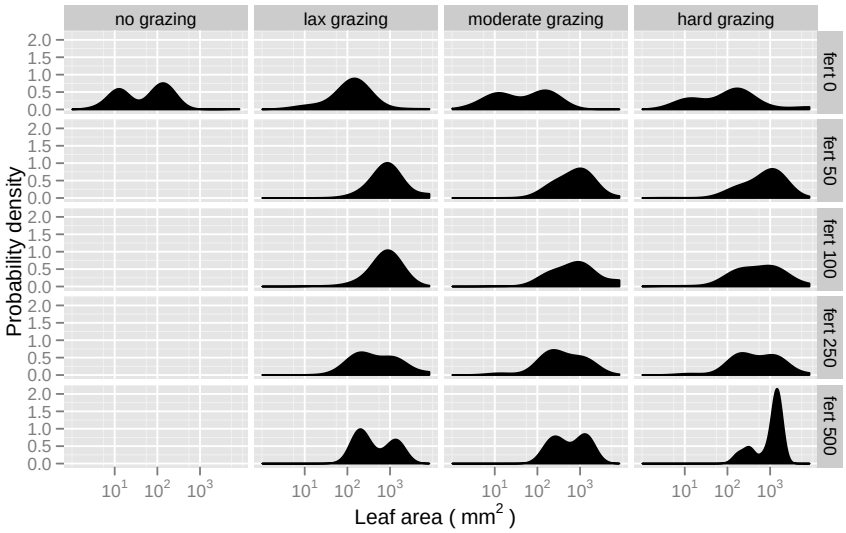

Figure 4.18: Abundance-weighted leaf area (LA) distributions across the experimental treatments. Each distribution is an average of two plots (replicates). The x-axis is on a logarithmic scale.

trend towards under-dispersion for leaf area under lax grazing than under the two higher grazing intensities (Table 4.5). Such reduced dispersion was particularly obvious in the leaf area distributions for the 0, 50, and 100 kg ha^{-1} yr^{-1} fertiliser treatments (Fig. 4.18).

For FEve, when LNC and height were considered simultaneously there was a significantly greater trend towards over-dispersion in the zero-fertiliser treatment relative to all other treatments, which actually showed trends towards under-dispersion (Table 4.4). When LNC was considered individually, there was a significant difference in deviations from the null FEve between the 100 and 500 kg ha^{-1} yr^{-1} treatments (Table 4.4). There was also a trend towards greater-than-expected FEve for LNC under lax grazing, while the opposite was found at the two other grazing intensities (Table 4.4). Finally, for height there was a trend towards lower-than-expected FEve under lax grazing, whereas the opposite was true under hard grazing (Table 4.4).

4.5 Discussion

The present study investigated shifts in the distribution of functional traits in plant communities from a long–running (27-year) experiment under contrasting availabilities of soil resources (i.e., P/S fertiliser and irrigation) and sheep grazing intensities after the initial sowing of a common mixture of 25 different pasture species (Scott, 1999). The focus of the investigation was on (i) the relationship among functional traits across plant species; (ii) the temporal dynamics of community-weighted traits across the different treatments; (iii) the direction and relative strength of selection on all traits across the different experimental treatments; and (iv) patterns of trait over- and under-dispersion within communities.

These four aspects of this study complement each other. First, it is necessary to explore trait inter-relationships and identify primary axes of functional variation at the species level to understand and explain shifts in trait distributions at the community level following environmental change (Suding et al., 2003); such shifts in trait distributions can be summarised by their expected trait values (i.e., community-weighted traits), thus reflecting changes in plant functional composition. Community-weighted traits, in turn, form the constraints in the maxent model, which enables us to quantify the relative importance of different traits in determining relative abundance (Shipley, 2010b; Sonnier et al., 2010a). Finally, exploring patterns of trait over- and under-dispersion can provide insights on the nature of assembly processes and mechanisms of species coexistence within communities (Mayfield and Levine, 2010). Each of these aspects are discussed separately in the following sections.

4.5.1 Relationships among Species Traits

Plant species were differentiated along two major axes of functional variation. The first and most important axis was mainly driven by LNC, LSC, SLA, LDMC, and to a lesser extent LPC. This axis represents the fundamental trade-off between traits that promote rapid growth and those that promote persistence (Chapin, 1980; Lambers and Poorter, 1992; Herms and Mattson, 1992; Aerts, 1995; Reich et al., 1997; Aerts and Chapin, 2000; Grime, 2002).

This nutrient acquisition–conservation trade-off has been identified as a primary axis of functional variation among species, both when several traits were compared across fewer species (Grime et al., 1997; Adler et al., 2004) and when fewer traits were compared across many species (Reich et al., 1997; Díaz et al., 2004; Wright et al., 2004). This axis separates competitors (C) and ruderals (R) from stress-tolerators (S) in Grime's (1974) CSR ecological strategy model, and is also one of the three axes in Westoby's (1998) leaf-height-seed (LHS) ecological strategy scheme.

Physiological reasons can explain why LNC, LSC, SLA, and LPC are associated with relative growth rate. Because photosynthetic enzymes account for $> 50\%$ of leaf N, LNC strongly controls photosynthetic rate, which itself is an important component of relative growth rate (Lambers et al., 2008a). S is an important component of proteins and other organic compounds, and plant requirements are tightly linked to growth rate (Hawkesford, 2007). SLA is correlated to relative growth rate (Poorter and Remkes, 1990; Garnier, 1992) because it expresses the area available for light interception per unit leaf dry mass, thus influencing photosynthetic rate (Dijkstra and Lambers, 1989); however, a meta-analysis showed that the relative importance of SLA vs that of net assimilation rate (correlated with photosynthetic rate) decreases as light intensity increases (Shipley, 2006). Finally, LPC is linked to relative growth rate because greater investments in P-rich ribosomes and rRNA are required to sustain rapid growth (Elser et al., 1996).

Although greater LNC, SLA, and LPC generally lead to higher relative growth rate, they are also associated with shorter leaf lifespan (Reich et al., 1992). On the other hand, LDMC, which depends on leaf density (Garnier and Laurent, 1994), is negatively correlated to relative growth rate (Garnier, 1992; Poorter and Bergkotte, 1992; Garnier et al., 1999) because higher leaf density results in smaller tissue volume and correspondingly low leaf area per unit dry mass (Ryser and Lambers, 1995; Ryser and Aeschlimann, 1999), unless compensated for by a reduction in leaf thickness. However, higher leaf density (and thus higher LDMC) leads to longer leaf lifespan (Ryser, 1996), presumably because it reflects a greater investment in sclerenchyma and vascular tissues (Dijkstra and Lambers, 1989; Garnier and Laurent, 1994; Van Arendonk and Poorter, 1994). Consequently, the trait

inter-relationships among the species found in this study provide further support for the proposition that the nutrient acquisition–conservation trade-off (Chapin, 1980; Lambers and Poorter, 1992; Aerts and Chapin, 2000) represents a fundamental axis of functional variation among plant species (Díaz et al., 2004; Wright et al., 2004; Laughlin et al., 2010).

Along this nutrient acquisition–conservation axis, native species in this study were functionally distinct from exotic species, with exotic species exhibiting a rapid-growth trait syndrome, while the reverse was true for natives. These results are consistent with those from a recent global meta-analysis comparing leaf traits among co-occurring exotic and native species, where exotic species were positioned further along the acquisition–conservation axis towards a faster-growth strategy (Leishman et al., 2007). The difference in leaf traits between native and exotic species observed in this study may be partly explained by the fact that all sown species at the start of the experiment were exotic species which had been selected based on their potential suitability as pasture species, of which high intrinsic growth rate is a key characteristic. Other studies that compared co-occurring herbaceous native and exotic species in New Zealand grasslands also found that exotic species had faster intrinsic growth rates compared with native ones (Scott, 1970; King and Wilson, 2006) or possessed leaf and root attributes associated with faster growth rates (Craine and Lee, 2003). This may reflect the particular evolutionary history of New Zealand grasslands, which prior to human settlement were confined to sites with marginal environmental conditions (McGlone, 2001).

The second major axis of functional variation among species was best represented by plant height, a result similar to that of Díaz et al. (2004) and Adler et al. (2004). Plant height is an important aspect of competitive ability (Grime, 1977; Gaudet and Keddy, 1988) when competition is primarily for light (Aerts, 1999). However, while taller species may be able to capture a greater proportion of light resources, frequent and/or intense disturbances can remove a disproportionate amount of their biomass relative to shorter species, putting them at a disadvantage (Grime, 2002). Therefore, allocation of aboveground biomass to occupy vertical space reflects another trade-off in plant functional variation that is influenced by distur-

bance frequency/intensity, and which is largely independent of the nutrient acquisition–conservation trade-off (Westoby, 1998; Grime, 2002; Díaz et al., 2004). Unlike the first principal component, there was no clear distinction between native and exotic species in this study along the second principal component, although the shortest species were primarily native.

4.5.2 Shifts in Community-Weighted Traits

Responses to Fertilisation

The first five years of the experiment were characterised by rapid shifts in community-weighted traits that reflected changes from more conservative nutrient economy strategies (lower SLA_{cw}, LNC_{cw}, LPC_{cw}, and LSC_{cw}, but higher $LDMC_{cw}$) to more acquisitive strategies at all fertiliser levels, with the trend most pronounced in the high fertiliser/irrigated treatment. These initial rapid shifts in community-weighted traits at all fertiliser levels were linked to marked increases in the relative abundance of species with N-fixing ability possessing leaf attributes associated with rapid growth, namely *L. polyphyllus* and clovers (*Trifolium* spp.). The increase in *L. polyphyllus* was particularly important in the dryland fertilised treatments (50, 100, and 250 kg ha^{-1} yr^{-1}), and to a lesser extent in the zero-fertiliser treatment, but not in the high fertiliser/irrigated treatment. On the other hand, clovers became largely dominant in the high fertiliser/irrigated treatment (although there was a shift in time from *T. repens* to *T. ambiguum*; Scott, 2007), but were less important in the dryland fertilised treatments. Since the fertiliser used in this study was sulphur-enriched superphosphate (i.e., a P/S fertilizer typical of legume-based pasture systems in Australia and New Zealand; Walker et al., 1955; Ludecke, 1962; Scott, 1999), the rapid increase in these N-fixing species in fertilised treatments can be explained by the strong dependency of N-fixation on P (Israel, 1987; Schulze et al., 1999; Olivera et al., 2004) and S (Walker et al., 1955; Scherer and Lange, 1996; Krusell et al., 2005; Varin et al., 2010), at least for crop legume species (Sprent, 1999). On the other hand, the initial rapid increase in the relative abundance of *L. polyphyllus* in the zero-fertiliser treatment may be partly due to this species exhibiting the same P acquisition strategy as congeneric *L. angustifolius*, which can release

large amounts of carboxylates through root exudation to solubilize P when it is deficient (Hocking and Jeffery, 2004).

Five years after the start of the experiment, decreases in SLA_{cw} and LNC_{cw}, and increases in $LDMC_{cw}$, were observed at all fertiliser levels, particularly at the highest one. SLA_{cw}, arguably the community-weighted trait that best reflects community-weighted intrinsic relative growth rate, decreased markedly, particularly in the high fertiliser/irrigated treatment. As a result, all treatments receiving fertiliser converged to a similar value ($\sim$ 20 m^2 kg^{-1}) at about year 15 and remained stable thereafter. These shifts stemmed from an increase in the relative abundance of grasses at the expense of the N-fixing species. One possible explanation for this pattern is that the build-up of soil N from N-fixing species, which was strongly dependent on fertiliser rate, coupled with ongoing sheep grazing pressure (and associated trampling), may have gradually favoured grasses over N-fixing species.

After its short-term (i.e., 0–5 year) rapid increase, SLA_{agg} in the zero-fertiliser treatment progressively decreased and eventually came back to its initial low value of $\sim$ 12 m^2 kg^{-1}. In fact, in the zero-fertiliser treatment all other leaf traits that were tightly related to leaf nutrient economy (i.e., LNC_{cw}, LPC_{cw}, LSC_{cw}, and $LDMC_{cw}$) also progressively reverted back to their original values, although this was a gradual process that occurred over a period of about 20 years. The rapid initial shift to a more nutrient-acquisitive, rapid-growth strategy (e.g., higher SLA_{cw}, LNC_{cw}, LPC_{cw}, and LSC_{cw}, but lower $LDMC_{cw}$) in the zero-fertiliser treatment was associated with marked increases in the relative abundance of *L. polyphyllus*, and, to a lesser extent, clovers.

The gradual return of the zero-fertiliser treatment towards its initial community-weighted trait values (e.g., low SLA_{cw}) supports the idea that nutrient limitation gives a long-term advantage to species with attributes that limit nutrient losses to herbivory and other stresses (Chapin, 1980; Ryser, 1996; Aerts and Chapin, 2000; Grime, 2002). Such attributes reduce growth rate (Lambers and Poorter, 1992; Ryser and Lambers, 1995), but can also lower acceptability to sheep (as evidenced by the gradual decrease in acceptability to sheep in the zero-fertiliser treatment after its initial peak) and

reduce nutrient losses by a slower tissue turnover rate. This interpretation is in line with microcosm experiments that showed how fast-growing plant species out-compete slow-growing ones under low-fertility conditions in the absence of generalist herbivores, but that the reverse is true when herbivores are present (Fraser and Grime, 1999; Buckland and Grime, 2000). As a result, 26 years after the start of the experiment, there was a large difference between the zero-fertiliser treatment and all other fertiliser levels for some community-weighted traits related to nutrient economy (i.e., SLA_{cw}, LSC_{cw}, LNC_{cw}), yet there were no differences among the treatments that received fertiliser (i.e., 50, 100, 250, and 500 kg ha^{-1} yr^{-1}). All treatments that received fertiliser were dominated by exotic grasses and clovers, whereas the zero-fertiliser treatment, though briefly having a component of sown species, returned back more or less to its original composition, albeit with the addition of some exotic grasses and *L. polyphyllus*.

Responses to Grazing Intensity

Compared to the large effects of soil resource availability on community-weighted traits, relative grazing intensity had much subtler effects, but these became more apparent with time. After 26 years, H_{cw} was greater under lax grazing than under moderate or hard grazing. This pattern agrees with a recent global analysis of plant trait responses to grazing (Díaz et al., 2007c) and supports the general idea that lower disturbance intensity/frequency favours attributes that increase competitive ability, such as greater plant height (Westoby, 1998; Bullock et al., 2001; Grime, 2002). For example, in French sub-alpine grasslands, Quétier et al. (2007b) found that H_{cw} increased following conversion from mowing (which they consider a more intense disturbance) to grazing (a less intense one). Similarly, Louault et al. (2005) showed that H_{cw} was greater under lower herbage use (i.e., sheep grazing) than moderate or higher herbage use (i.e., more intense grazing and cutting). Given that the differences in disturbance regimes in these previous two studies were much more contrasted (and of a different nature, i.e., mowing vs grazing) than the relative grazing intensities used in the present study, it is noteworthy that differences in H_{cw} were still detected.

Higher grazing intensity led to greater LNC_{cw}, LPC_{cw}, LSC_{cw}, and lower $LDMC_{cw}$, suggesting that species with traits associated with a rapid-growth strategy become more prevalent under higher grazing intensity. The prevalence of such a grazing-tolerant strategy under more intense grazing has also been reported elsewhere (Cingolani et al., 2005; Cruz et al., 2010). Westoby (1999) suggested that low-intensity, selective grazing should favour slower-growing, less palatable plants (grazing avoidance), whereas hard non-selective grazing should favour faster-growing, more palatable plants (grazing tolerance). Since all plots used in this study were "mob-grazed" (i.e., a large number of sheep were introduced to plots for 3–4 days), these results support Westoby's (1999) suggestion. However, in the high fertiliser/irrigated treatment LPC_{cw} and LSC_{cw} were significantly greater under hard grazing than under lax grazing. These significant fertiliser × grazing interactions support the resource availability model (Coley et al., 1985), which predicts that a rapid-growth, grazing-tolerant strategy, becomes more advantageous under greater resource availability.

4.5.3 Selective Advantage of Traits

Despite providing some insights, testing for differences in community-weighted traits does not inform us on the direction of selection exerted on particular traits (e.g., does greater SLA lead to greater relative abundance?), nor on the relative strength of selection (e.g., is a higher SLA more important under some environmental conditions than others?). This is because the direction and strength of selection must be defined by reference to the entire pool of species that could potentially colonise a site, including those that did not successfully establish (Shipley, 2010b). For example, sites with higher soil resource availability could show higher SLA_{cw}, yet the direction of selection on SLA could still be negative if the majority of species from the regional pool had very large SLA values and if these species were absent or present only at very low abundance in these sites. Moreover, SLA_{cw} would be a constraint to community assembly, rather than simply a consequence of community assembly, only if the relative abundances that are predicted in its presence in the model differ from those that are predicted in its absence

(Shipley, 2010b,a). For instance, particular values of SLA_{cw} may not reflect constraints on community assembly but instead simply arise from correlations with other important constraints, such as LNC_{cw}. On the other hand, the parameters of the maxent model (i.e., the λ-values) can be directly used to quantify the direction and relative strength of selection on different traits during community assembly (Sonnier et al., 2010a).

Prediction of Relative Abundances

The initial motivation for using the maxent model to community assembly was not to predict species abundances (e.g., Shipley et al., 2006b; Sonnier et al., 2010b; Mokany and Roxburgh, 2010), but instead to compare the λ-values of the maxent model among experimental treatments (Sonnier et al., 2010a). That said, for the λ-values to be meaningful, the model must first be able to predict accurately the observed relative abundances. Using all traits except leaf thickness and a uniform prior, 66% of the variation in the relative abundances of the 51 species from the regional pool over 32 plots could be explained. This value is substantially less than the first empirical application of the model, which predicted 96% of the variation in the relative abundances of 30 species from 12 plots, using 8 traits and a uniform prior (Shipley et al., 2006b). One potential explanation for this poorer fit is simply that the community-weighted traits used in this study reflect weaker constraints over community assembly. However, Shipley et al. (2006b) used a subset of species from the regional pool, excluding very rare ones, whereas complete botanical surveys, and associated trait data for all species, were used in this study. Reducing the number of rarer species increased the predictive capacity of the maxent models. This suggests that the relative abundances of rarer species are only weakly determined by the traits included in the model. Recently, it has been pointed out that the influence of incomplete surveys and missing species on the predictive capacity of maxent is as yet unknown (He, 2010); these results indicate that this effect can be large. Since the measure of relative abundance used in this study, based on visual cover estimates, is necessarily less precise than actual biomass estimates, this lower precision also likely contributed to the remaining lack of fit in the models.

Relative Importance of Traits across Treatments

In an effort to increase to predictive capacity of the full maxent model that included all species, a more informative neutral prior was used. In addition, leaf thickness was added as a trait in the model because this trait can vary independently of LDMC or SLA along environmental gradients (Witkowski and Lamont, 1991). This more complex model had much greater predictive capacity, explaining 93% of the variation in relative abundances in all species from all plots even when the rarest species were included, and was used to compare its λ-values across experimental treatments.

In this model, selection on SLA became increasingly negative (i.e., species with larger SLA values were less abundant, holding other traits constant) as soil resource availability increased, although differences were only statistically significant between the zero-fertiliser and the high fertiliser/irrigated treatments. This contrasted sharply with the marked and highly significant increase in SLA_{cw} following fertiliser addition. However, because λ-values reflect the selective pressure on single traits after taking into account other traits included in the model, the results for SLA need be interpreted accordingly, particularly since SLA is a product of leaf thickness and LDMC (Witkowski and Lamont, 1991; Vile et al., 2005). First, there was a trend for leaf thickness to be less negatively selected against under greater soil resource addition, although differences between fertiliser levels were not significant. However, given the similarity of the patterns found for leaf thickness and SLA (for which significant differences between fertiliser levels were found), and the clear monotonic decrease in λ-values for leaf thickness with fertiliser rate, the inability to reject the null hypothesis for leaf thickness likely reflects more the lower statistical power for tests of a whole plot factor (here, fertiliser level) in a split-plot design (Gotelli and Ellison, 2004) than a true null hypothesis. Second, selection on LDMC was absent across all fertiliser treatments with the exception of the 50 kg ha^{-1} yr^{-1} treatment, where selection was positive. Therefore, one possible interpretation for these results was that although species with increasingly thinner leaves were selected for under greater soil resource availability, further increasing SLA of thinner leaves was selected against because this can only arise through a lower LDMC. A

lower LDMC may be disadvantageous under grazing, since a greater investment in cell wall material (and thus greater LDMC) can confer resistance against trampling (Lambers et al., 2008a). While lower leaf thickness can increase the rate of CO_2 diffusion inside the leaf (Syversten et al., 1995), thus potentially promoting photosynthesis, it seems unlikely that this alone can explain the selective advantage of lower leaf thickness under greater soil resource availability. Rather, it may be interpreted as a way to maximise SLA (and thus maximise light interception per unit leaf dry mass) without sacrificing LDMC (and thus maintain leaf structural defenses). In French grasslands, Sonnier et al. (2010a) have also observed such a parallel selection for species with thin but dense leaves in fertilised and grazed grasslands. Whether this might represent a general strategy for plant survival in fertile grasslands under grazing requires further study.

The ability to symbiotically fix atmospheric N conferred greater fitness in all treatments that received fertiliser, whereas selection on this trait was absent in the zero-fertiliser treatment. Similarly, the selection on LSC in fertilised treatments was positive, whereas it was absent in the zero-fertiliser treatment. These results agree with the patterns that were found for NF_{cw} and for LSC_{cw}. Remembering that the fertiliser applied was S-enriched superphosphate (i.e., a P/S fertiliser), the interpretations thus remain similar to those put forward for the patterns in community-weighted traits. First, N is a crucial element for photosynthetic enzymes and thus strongly controls photosynthetic rates (Lambers et al., 2008a), and N enters natural ecosystems predominantly through fixation of atmospheric N (Chapin et al., 2002). However, since N fixation strongly depends on P (Israel, 1987; Schulze et al., 1999; Olivera et al., 2004) and S (Scherer and Lange, 1996; Krusell et al., 2005; Varin et al., 2010), at least in crop legume species (Sprent, 1999), this may explain why this trait conferred greater fitness only in the presence of the P/S fertiliser. Second, higher soil resource availability favours a rapid-growth, nutrient-acquisitive strategy (Aerts and Chapin, 2000), and greater LSC is associated with faster growth because of the importance of S in proteins and other organic compounds (Hawkesford, 2007). Sulphur (S) deficiency is widespread in many areas of New Zealand, especially in drier inland areas (Walker and Gregg, 1975), and S is a key limiting nutrient to

pasture growth in the study area (Douglas and Risk, 1981; Scott, 2000f). Assuming that greater LSC reflects a greater capacity for S uptake, this may explain why LSC conferred greater fitness as S availability increases in fertilised treatments. On the other hand, under low S availability it may be more advantageous to conserve acquired S through greater constitutive defenses (e.g., lower SLA and/or higher LDMC, which would "dilute" LSC), and this may explain why selection on LSC was absent in this treatment. There was only a weak positive selection for LPC and no selection for LNC at all fertiliser levels, but this probably reflected the fact that all three traits were highly positively correlated between species, such that greater LPC or LNC conferred little additional benefit once LSC (and other traits) was taken into account. As shown before with leaf thickness, SLA, and LDMC, this highlights the importance of considering covariation between traits when interpreting the direction and strength of λ-values (Shipley, 2010b; Sonnier et al., 2010a).

Greater plant height conferred greater fitness under lower grazing intensity than under moderate or hard grazing, where selection on height was actually negative. This was consistent with the results found for H_{agg}. A likely explanation is that under higher disturbance intensity/frequency, taller species lose a disproportionate amount of their aboveground biomass relative to shorter ones, whereas lower disturbance intensity/frequency can favour taller species because greater height is associated with greater competitive ability (Westoby, 1998; Bullock et al., 2001; Grime, 2002), at least when competition is primarily for light (Aerts, 1999). Greater LNC also conferred greater fitness under lower than harder grazing intensity, and greater leaf thickness was less negatively selected against under harder than lower grazing. Together, these results point towards a positive selection for tall species with a rapid-growth strategy (through higher LNC and thinner leaves), which fits well with the competitor strategy of Grime (1974). However, it must be noted that this contradicts the results found for community-weighted traits, where higher grazing intensity led to significantly greater LNC_{agg}, LPC_{agg}, LSC_{agg}, and lower $LDMC_{agg}$ (Fig. 4.7). This illustrates that there is not always a direct link between community-weighted traits, which are computed only from the species that are actually present at a site, and the λ-values of

the maxent model, which represent the direction and strength of selection on the entire available pool of species, including those that have already been excluded from the local community (Shipley, 2010b).

Model Parsimony

Can we identify a parsimonious set of traits that are most important in driving community assembly? To try and answer this question, a simple backward selection procedure was used, where traits with the smallest absolute average λ-values across all plots were progressively removed from the models. This approach suffers from many of the same drawbacks as standard forward or backward stepwise approaches to variable selection in regression models. For example, not all model subsets can be tested, and high collinearity between traits can lead to unstable solutions (Shipley, 2010b). However, no alternatives are currently available for selection of maxent models, and only forward or backward stepwise approaches have been used so far (Shipley, 2010b; Mokany and Roxburgh, 2010; Sonnier et al., 2010a). Despite the limitations of the backward stepwise approach, it was clear that some traits such as LCC and lifespan were never important constraints to community assembly in these grasslands, and could be omitted in future studies of grassland responses to fertilisation and/or grazing. The irrelevance of LCC to community assembly in grazed French grasslands under contrasting fertiliser and grazing intensity regimes was also noted by Sonnier et al. (2010a). Second, LSC was always more important than LPC, which may reflect the limiting nature of S in these grasslands (Douglas and Risk, 1981; Scott, 2000f). Third, the maxent model without leaf thickness increased the importance of LNC and LDMC, two traits that were also found to be important by Sonnier et al. (2010a). On the other hand, in the other models that included leaf thickness, LDMC and LNC became unimportant, while correlated traits such as SLA and LSC became more important. This illustrates the difficulty of getting stable estimates λ-values when relatively high collinearity among traits is present (Shipley, 2010b). Consequently, the development of more sophisticated procedures for trait selection in maxent models is an important area for future research. Nevertheless, although achieving model parsimony is a

worthwhile goal, it is questionable whether the maxent model could achieve accurate predictions of species relative abundances with very few traits, since some have argued that species coexist in communities because they differ functionally from each other in many dimensions (Clark et al., 2007).

4.5.4 Trait Over- and Under-Dispersion

In the previous sections, the focus was on how trait-based community assembly across different environmental conditions is associated with shifts in community-weighted traits (i.e., trait means), and whether these trait means reflect constraints to community assembly. However, trait-based habitat filtering during community assembly does not only affect the means of trait distributions but also their dispersion or spread (Weiher and Keddy, 1995; Kraft et al., 2008; Cornwell and Ackerly, 2009; Webb et al., 2010). To reiterate, trait over-dispersion is defined here as an observed functional diversity metric that is greater than the null expectation from an abundance-based null model of random community assembly, whereas trait under-dispersion is less than the null expectation.

Trait Under-Dispersion under High Soil Resource Availability

There was strong evidence for trait under-dispersion at the highest level of soil resource availability (i.e., high fertiliser/irrigated treatment). In those plant communities, multivariate trait volumes were much smaller than expected under a null random model, indicating that community membership was restricted to a reduced subset of ecological strategies relative to those found across the entire species pool. This result held when only LNC and height (the two traits that best expressed the first two principal components) were considered, and was also found for some individual traits (i.e., LDMC, LNC, leaf area). The strong trait under-dispersion in the high fertiliser/irrigated treatment was largely due to the disappearance of (i) all short, slow-growing (i.e., low LNC) native species; (ii) *Hieracium pilosella*, the short exotic species with moderately high LNC that dominated all plots prior to the start of the experiment; and (iii) *Festuca novae-zelandiae* and *Poa colensoi*, two relatively tall native tussock grass species with traits asso-

ciated with slow growth rates.

In trait-based community assembly analyses, a restricted range (or restricted multivariate volume) in functional attributes has generally been attributed to abiotic environmental filtering, whereby unusually stressful abiotic conditions only allow species with evolved tolerances to these conditions to persist in the community (van der Valk, 1981; Weiher and Keddy, 1995; Weiher et al., 1998; Cornwell et al., 2006; Kraft et al., 2008; Cornwell and Ackerly, 2009; Ingram and Shurin, 2009). However, given that strong under-dispersion was observed in the treatment with the most favourable conditions for plant growth (i.e., highest fertiliser input and irrigation), this interpretation seems unlikely. Rather, such under-dispersion probably resulted from asymmetric competition for soil resources from faster-growing species, leading to the competitive exclusion of plant species with inherently slower growth, particularly those of short stature (with associated small leaves). Similarly, Mayfield and Levine (2010) have argued that competitive exclusion can lead to trait under-dispersion when species differences in competitive ability overcome niche differences.

Trait Over-Dispersion under Low Soil Resource Availability

In contrast to the restricted range in trait values and multivariate trait volumes found under the treatment with the greatest availability of soil resources, there was strong evidence for trait over-dispersion under the lowest soil resource availability. Indeed, in the zero-fertiliser treatment, abundance was over-dispersed along LPC and LCC axes (i.e., greater than expected FDis), and it was also more evenly spread than the other fertiliser treatments in a two-dimensional trait volume composed of LNC and height (i.e., greater than expected FEve). The percent cover data indicated that the observed over-dispersion could be explained by the relatively equal representation of the following groups of species, with contrasting ecological strategies: (i) *H. pilosella*, a species with moderately high leaf nutrient concentrations and SLA, and with relatively high acceptability to sheep but not heavily grazed due its prostrate growth form; (ii) exotic grasses, generally with moderately high leaf nutrient concentrations but with greater height than *H.*

pilosella (thus being more available to sheep); (iii), the two native tussock grass species *F. novae-zelandiae* and *P. colensoi*, with low nutrient concentrations and SLA, high LDMC, and low acceptability to sheep, but relatively high height; and (iv) other species, mostly of small stature and with leaf attributes associated with slow growth, and largely uneaten by sheep.

Trait over-dispersion in plant communities has generally been interpreted as evidence for the dominant role of competitive interactions in structuring communities (Weiher and Keddy, 1995; Weiher et al., 1998; Stubbs and Wilson, 2004), whereby strong competition for resources entails limiting similarity with respect to strategies of resource acquisition and use (MacArthur and Levins, 1967). This interpretation may seem at odds with the view that competition intensity decreases with lower productivity and becomes relatively unimportant for community assembly in nutrient-poor environments (Grime, 2002). However, this view may be reconciled if we accept that the *intensity* of competition is not necessarily related to its *importance* in structuring communities (Welden and Slauson, 1986; Aerts, 1999). The observed trait over-dispersion under the lowest soil resource availability may occur precisely because competition is important but not intense, such that it promotes the coexistence of alternative designs of approximately equal fitness (Chesson, 2000; Marks and Lechowicz, 2006) for acquiring nutrients and reducing their loss to grazing, with no particular strategy strongly outperforming the others. This view is supported by the fact that few traits stood out as having large absolute λ-values in the zero-fertiliser treatment compared to the other fertiliser levels. This contrasts sharply with the strong under-dispersion observed under the highest soil resource availability due to the competitive exclusion of species with a nutrient-conservation strategy, and to community-wide convergence towards a rapid-growth strategy.

Trait Dispersion and Species Coexistence

Exploring shifts in the dispersion of trait distributions may help to explain why some communities sustain more species than others. For example, it has been hypothesised that a greater number of limiting resources allows more opportunities for trade-offs between mechanisms of resource-acquisition, thus

allowing a greater number of species to coexist (Tilman, 1988; Harpole and Tilman, 2007). Assuming that the traits used are proxies reflecting overall strategies of resource acquisition, a greater number of resource acquisition strategies within a community should be reflected by a greater functional trait volume. Consistent with this hypothesis, functional trait volumes decreased sharply with fertiliser addition, and were smallest in the high fertiliser/irrigated treatment. These decreases in trait volumes were associated with decreasing species richness, except in the high fertiliser/irrigated treatment, where species richness was similar to the other fertilised treatments despite showing smaller than expected trait volumes. This may haven arisen because the species pool was augmented with fast-growing species through sowing at the start of the experiment, as several of these species were located within the trait volumes of the high fertiliser/irrigated treatment. In addition, the high fertiliser/irrigated treatment sustained the highest net sheep grazing days achieved because of its highest plant production (results not shown), and grazing by large mammalian herbivores can increase plant diversity by suppressing competitively dominant (i.e., taller) species (Olff and Ritchie, 1998). This latter point may also partly explain why there was a small but significant overall decrease in plant species richness under the lowest grazing intensity compared to the other two grazing intensities, which is consistent with the view that low disturbance frequency or intensity can promote competitive exclusion and decrease species richness (Grime, 1973).

Weiher et al. (1998) suggested that among plant communities, the sizes of functional trait volumes should stay relatively constant, such that they would not scale positively with plant species richness. However, they argued that increasing soil resource availability would increase competition intensity, which in turn would increase the mean distance between neighbouring species in trait space. If functional trait volumes are constant, they concluded that this would necessarily reduce the number of species that can coexist in the community (Weiher et al., 1998). Contrary to their hypothesis, functional volumes did scale with species richness in this study. Strong competition intensity at the highest soil resource availability did not lead to trait overdispersion due to limiting similarity, but instead led to markedly smaller trait volumes because of the competitive exclusion of particular strategies.

On the other hand, low soil resource availability led to greater trait volumes (and corresponding higher species richness), yet abundance was markedly over-dispersed along particular functional axes, a signature of limiting similarity. These results therefore suggest that limiting similarity may be particularly important in determining community structure and species richness in low-resource environments, where competition is important but not intense, whereas in high-resource environments greater competition intensity may exclude those species with traits that do not confer high competitive ability, thus potentially reducing species richness.

4.6 Conclusions

By experimental additions to the plant species pool, manipulation of soil resource availability and grazing intensity, and long-term (27-year) monitoring of shifts in trait distributions across experimental treatments, insights into some of the key questions in trait-based research were obtained. First, the results provide further support for the importance of the nutrient acquisition–conservation trade-off as a primary axis of functional variation among plant species (Grime et al., 1997; Díaz et al., 2004; Wright et al., 2004), and for the presence of differences between native and exotic species along that axis (Leishman et al., 2007). Second, this study provides long-term experimental support for the hypothesis that slow-growing species become dominant under nutrient-poor environments because they hold a long-term advantage through leaf attributes that reduce nutrient losses (Chapin, 1980; Ryser, 1996; Aerts and Chapin, 2000; Grime, 2002). Third, the relative abundances of plant species from a common initial species pool were strongly influenced by functional traits across all experimental treatments, highlighting the importance of traits in determining relative abundance (Shipley et al., 2006b; Shipley, 2010b; Cornwell and Ackerly, 2010). Fourth, the direction and strength of selection on particular traits shifted with soil resource availability and sheep grazing intensity (Sonnier et al., 2010a), showing how different trait-based filters act under different environmental conditions. Finally, high soil resource availability led to strong trait under-dispersion due to competitive exclusion, whereas low soil resource availability led to trait over-dispersion

due to limiting similarity. This challenges previous interpretations that trait under-dispersion should be more prevalent under increasing environmental stress, whereas limiting similarity should be more important in productive environments where competition intensity is greatest (Weiher and Keddy, 1995; Weiher et al., 1998).

This study combined analytical approaches that have generally been used in isolation in trait-based community assembly research, namely: (i) the study of patterns in community-weighted traits along environmental gradients (e.g., Louault et al., 2005; Quétier et al., 2007b; Garnier et al., 2007; Díaz et al., 2007a; Gross et al., 2008); (ii) the use of null models to test for trait over- or under-dispersion (e.g., Stubbs and Wilson, 2004; Cornwell et al., 2006; Kraft et al., 2008; Cornwell and Ackerly, 2009; Ingram and Shurin, 2009); and (iii) the use of maxent models to predict species abundances at local communities (e.g., Shipley et al., 2006b; Sonnier et al., 2010b; Mokany and Roxburgh, 2010) and to compare selective advatange of different traits across different environments (Sonnier et al., 2010a). These approaches are complementary and would benefit from being integrated more tightly in future studies. First, community-weighted traits represent the constraints to community assembly in maxent models (Shipley, 2010a), and prediction of expected values of trait distributions across space and time is a promising avenue for predicting feedbacks on ecosystem function (Webb et al., 2010) and community structure (Shipley et al., 2006b; Shipley, 2010b). Second, exploring patterns of trait dispersion can provide insights on how biotic interactions influence community assembly (Gross et al., 2009). If the variance of trait distributions were to vary predictably along environmental gradients, the predictive capacity of the maxent model could be enhanced since constraints on trait variances can be easily specified in the model (Shipley, 2010b). Consequently, using constraints on trait means and variances in conjunction with informative "neutral" priors in maxent models may offer a coherent methodological framework for assessing the relative importance of traits, biotic interactions, and propagule pressure in determining the relative abundances of species at local communities.

Some limitations of this study also highlight future challenges for trait-based community assembly research. First, the focus was largely on above-

ground functional traits, primarily because of their ease of measurement, yet belowground traits (e.g., specific root length, average rooting depth, presence of specialized root structures) could be very important in determining community structure, especially in nutrient-poor soils (Aerts, 1999; Lambers et al., 2008b). Chemical traits involved in defence against herbivores could also be important (e.g., Funk and Throop, 2010) but have been neglected in trait-based community assembly research. Second, several of the traits used were strongly inter-correlated, which led to unstable solutions in the selection procedure for maxent models and also complicated interpretation. As a result, future studies should aim at measuring traits that reflect as many independent axes of functional variation as possible. Lastly, there is a clear need to develop better model selection approaches for maxent models than the simple stepwise procedure used in this study (He, 2010).

Despite these limitations, this study suggests a way forward to understand and describe changes in plant species composition and diversity under land-use change in grazing systems (Chapin et al., 2000). This is crucial because land-use change is expected to be the single most important driver of changes in biodiversity worldwide for this next century (Sala et al., 2000). In particular, pastures and rangelands cover 25% of the ice-free surface of the Earth (Asner et al., 2004) and are expected to undergo rapid intensification (Bouwman et al., 2005) to meet the forecasted doubling in global food demand by 2050 (Alexandratos, 1999), and increased demand for meat from developing countries in particular (FAO, 2005). In that regard, this study highlights the importance of considering species functional differences to understand how plant communities react to increases in soil resource availability and increasing intensity and frequency of biomass removal, two important and often inseparable components of land-use change.

Chapter V

Cascading Effects of Long-Term Land-Use Changes on Plant Traits and Ecosystem Functioning[1]

5.1 Summary

Land-use changes alter ecosystems worldwide, yet such changes have been largely ignored in biodiversity-ecosystem function experiments. In this Chapter, it is shown that long-term (27-year), realistic manipulations of soil resource availability and grazing intensity in grasslands cause shifts in plant functional composition and diversity, with cascading effects on multiple ecosystem processes. Resource availability exerted dominant control over aboveground production and decomposition, both directly and indirectly via plant trait shifts. Importantly, increasing resource availability moderated the impacts of grazing intensity and plant functional diversity on these processes, shifting them both from negative to positive. These changes in turn altered soil respiration and soil carbon sequestration. This study reveals that human changes to resource availability and grazing pressure directly, indirectly, and interactively control ecosystem functioning and carbon sequestration.

5.2 Introduction

There is growing concern about how human-induced changes in biodiversity (Pimm et al., 1995; Pimm and Raven, 2000; Sala et al., 2000) will affect ecosystem functioning – the rates of processes that control the flow of energy and matter across ecosystem compartments (Chapin et al., 1997, 2000;

[1] This Chapter has been submitted as:
Laliberté, E. and Tylianakis, J. M. (submitted). Cascading effects of long-term land-use changes on plant traits and ecosystem functioning.

Hooper et al., 2005; Balvanera et al., 2006; Díaz et al., 2006). While it is clear that biota control the transfers of energy and matter within ecosystems (Chapin et al., 1997, 2000; Hooper et al., 2005), there has been considerable debate (Aarssen, 1997; Huston, 1997; Hodgson et al., 1998; Wardle et al., 1998; Huston et al., 2000; Srivastava and Vellend, 2005; Duffy, 2009) over the interpretation and relevance of early experiments claiming positive effects of species richness and ecosystem functioning (e.g., Naeem et al., 1994; Tilman and Downing, 1994; Tilman, 1996; Hector et al., 1999). In particular, it has been argued that the random species assemblages used in these experiments do not reflect the non-random changes in biodiversity that occur following environmental perturbation (Leps, 2004; Srivastava and Vellend, 2005; Schläpfer et al., 2005), and that effects may be driven by functional traits of the dominant species rather than species richness *per se* (Huston, 1997; Grime, 1998; Mokany et al., 2008). Some have also argued that timescales of experiments have often been too short to provide useful insights (Thompson et al., 2005), and that longer-term perspectives are needed (Symstad et al., 2003; Hooper et al., 2005). Finally, effects of diversity on ecosystem functioning may be weak relative to the environmental forces or management practices that directly alter ecosystem functioning, as well as driving biodiversity loss (Huston and McBride, 2002; Schaffers, 2002; Srivastava and Vellend, 2005; Kahmen et al., 2005; Grace et al., 2007).

Surprisingly, even though the vast majority of these experiments have been conducted in grasslands (Balvanera et al., 2006), the increases in agricultural inputs (e.g., fertilisation, irrigation) and grazing pressure that drive change in grasslands worldwide (Bouwman et al., 2005) have been largely ignored (Sanderson et al., 2004). Yet, land-use change is expected to be the greatest global driver of biodiversity loss for this century (Sala et al., 2000), and biotic changes may be only one of the pathways through which land use alters the functioning of ecosystems (Chapin et al., 2000; Hooper et al., 2005; Srivastava and Vellend, 2005; Grace et al., 2007). As a result, it is widely recognised that we must move beyond simply asking whether biodiversity matters to the functioning of ecosystems, but instead ask how it matters, and by how much (Naeem and Wright, 2003; Srivastava and Vellend, 2005; Díaz et al., 2007a; Reiss et al., 2009; Hillebrand and Matthiessen, 2009).

This study shows that long-term (27-year), realistic manipulations of soil resource availability and grazing intensity in experimental grasslands drive changes in plant functional composition and diversity, with cascading direct and indirect effects on primary production, litter decomposition, soil respiration, and soil carbon sequestration. The experiment consisted of the initial sowing of a common plant species pool (25 species) into resident grassland vegetation (30 large 8×50-m plots) in 1982, with annual manipulations of soil resource availability (five fertilisation levels, with the lowest receiving no fertiliser, and the highest also being irrigated) and sheep grazing intensity (three levels, leading to different proportions of aboveground net primary production [ANPP] grazed). This long-term experiment thus represents a realistic gradient of land-use intensification in grazing systems (Bouwman et al., 2005) – the most extensive land use on Earth (Asner et al., 2004; Foley et al., 2005).

In grasslands, soil resource availability can control ecosystem functioning either directly (Burke et al., 1997), or indirectly via shifts in plant traits (Díaz et al., 2007a; Quétier et al., 2007b). Similarly, grazing intensity can exert direct control over ecosystem processes (McNaughton et al., 1997), or indirect control through shifts in plant composition (Bardgett and Wardle, 2003; Bagchi and Ritchie, 2010). Importantly, the direction and strength of grazing effects on vegetation and ecosystem processes are thought to depend on soil resource availability (Olff and Ritchie, 1998; Bardgett and Wardle, 2003). Moreover, effects of biodiversity on ecosystem functioning are also expected to vary with environmental context (Cardinale et al., 2000; Wardle and Zackrisson, 2005), particularly soil resource availability (Fridley, 2002) and disturbance (Cardinale et al., 2000). As a result, calls have been made for comprehensive experiments exploring direct and indirect herbivore impacts on aboveground and belowground processes in ecosystems of varying soil resource availability (Bardgett and Wardle, 2003), as well as for "next-generation" biodiversity-ecosystem functioning experiments that explicitly consider realistic drivers of change in biodiversity (Srivastava and Vellend, 2005; Hillebrand and Matthiessen, 2009), of which land-use change is the single most important one (Sala et al., 2000). The present study addresses both of these calls.

A response-effect trait framework is employed, which is best for exploring functional consequences of changes in biodiversity (Chapin et al., 2000; Lavorel and Garnier, 2002; Hooper et al., 2002; Naeem and Wright, 2003; Hooper et al., 2005; Díaz et al., 2007a; Suding et al., 2008). Community-weighted means (*sensu* Garnier et al., 2004; Díaz et al., 2007a) of two leaf traits are used as markers of functional composition: specific leaf area and leaf C:N ratio (hereafter, SLA and leaf C:N). These leaf traits have been shown to respond strongly to shifts in soil resource availability or grazing (Chapter 4), and are expected to influence ecosystem biogeochemical processes (Lavorel and Garnier, 2002; Garnier et al., 2004; Quétier et al., 2007b; Díaz et al., 2007a). Plant functional diversity was estimated using a broader range of leaf morphological and chemical traits, whereas chemical traits were used to explore potential effects of chemical diversity on litter decomposition (Epps et al., 2007; Meier and Bowman, 2008; Gessner et al., 2010).

The main hypothesis was that soil resource availability would have a dominant influence over ecosystem functioning through direct effects on production (Burke et al., 1997; Lambers et al., 2008a), indirect effects mediated via shifts in plant traits (Garnier et al., 2004; Quétier et al., 2007b), and by altering the strength and direction of the impacts of grazing intensity (Bardgett and Wardle, 2003). It was also hypothesised that higher grazing intensity would increase functional diversity by suppressing competitive dominance (Grime, 1973), and that such effects would be more pronounced under greater soil resource availability competitive exclusion is most likely (Olff and Ritchie, 1998; Aerts, 1999). However, functional (and chemical) diversity was expected to play only minor roles on ecosystem functioning relative to environmental drivers (Díaz et al., 2007a), although its effects could depend on resource availability (Fridley, 2002). Finally, it was hypothesised that grazing intensity would moderate effects of functional diversity on ecosystem functioning through greater disturbance (Cardinale et al., 2000), and because grazing can alter resource heterogeneity (Augustine et al., 1998), which can in turn alter the relationship between biodiversity and ecosystem functioning (Tylianakis et al., 2008).

In order to test such a complex, multifaceted causal hypothesis against alternative hypotheses, the strengths of long-term experimental controls were

Code	Variable	Units	Range
SRA	Soil resource availability	Unitless	1–5
GI	Grazing intensity (proportion of ANPP grazed; 18-month period)	Unitless	0.3–1.1†
SLA	Specific leaf area (community-weighted mean)	m^2 kg^{-1}	12.3–20.8
C:N	Leaf C:N ratio (community-weighted mean)	Unitless	12.0–23.4
FD	Functional diversity (multivariate dispersion)	Unitless	0.05–0.36
CD	Leaf chemical diversity (multivariate dispersion)	Unitless	0.03–0.31
ANPP	Aboveground net primary production (18-month period)	Mg DM ha^{-1}	1.7–34.3
BNPP	Belowground net primary production (18-month period)	Mg DM ha^{-1}	3.6–9.5
SR	Soil respiration	g C m^2 h^{-1}	0.3–1.6
ST	Soil temperature	°C	10.3–15.6
SC 0–20	Soil carbon (0–20 cm)	Mg DM ha^{-1}	57.4–110.9
SC 60–80	Soil carbon (60–80 cm)	Mg DM ha^{-1}	12.5–45.0
LD	Litter decomposition rate ($\hat{k} \times 10^3$)	Unitless	0.97–8.44

Table 5.1: Description of variables used in the analyses. †Values above 1 could be obtained because the measurement period started near peak standing biomass, but ended directly after all plots were grazed before the winter resting period (see details on page 134). DM = dry matter.

combined with statistical controls, using structural modelling (Shipley, 2009a). This approach offered a coherent, robust and flexible way to test for direct and indirect effects, while also considering potential non-linear effects (Grace et al., 2007) and interactions involving soil resource availability, grazing intensity, and functional or chemical diversity. Codes for all variables used in the analyses are listed in Table 5.1.

5.3 Materials and Methods

5.3.1 Study Area and Study Site

A detailed description of the study area and study site is given on page 34.

5.3.2 Experimental Design

A detailed description of the experimental design is given on page 34.

5.3.3 Vegetation Sampling

Sampling of all vascular plant species present within each plot was undertaken in November 2007 and 2008 (see Chapter 3). Twenty 1×1-m quadrats were randomly positioned along two longitudinal transects in each plot. Transects were 3 m apart from each other and 2 m from the closest fence to avoid edge effects. Cover (i.e., vertical projection of canopy, including living and non-living components) of all vascular plant species present in each 1×1-m quadrat was recorded using a seven-point semi-quantitative scale (1, $< 0.1\%$; 2, 0.1–0.9%; 3, 1–5%; 4, 6–25%; 5, 26–50%; 6, 51–75%; 7, 76–100%). Mean percent cover per species per plot was calculated by taking the median of the cover class for each species in each of the 20 quadrats, then averaging across these quadrats. Species present within the entire plot but not in the individual 20 1×1-m quadrats were assigned the lowest possible cover value (i.e., the median of cover class 1, divided by 20). Percent cover data per plot were transformed to relative abundances by dividing the percent cover of each species by the sum of percent cover values for all species present. Relative abundance data from 2007 and 2008 were averaged.

5.3.4 Plant Traits and Functional Diversity

A group of leaf traits were selected for this study; these traits have been identified as a suitable set of traits to predict plant species responses to environmental change and effects on ecosystem processes in herbaceous communities, while still being possible to measure across a wide range of species (Weiher et al., 1999; Lavorel and Garnier, 2002; Cornelissen et al., 2003; Lavorel et al., 2007; Garnier et al., 2007). Specific leaf area (SLA) and leaf

dry matter content (LDMC) were measured on at least 10 individuals per plant species (spread among the five fertiliser treatments, with a minimum of two individuals per fertiliser level), following a standardised protocol (Garnier et al., 2001). A composite sample of 10 individuals per species (spread among the five fertiliser treatments) was used to estimate leaf carbon concentration (LCC), nitrogen concentration (LNC), phosphorous concentration (LPC), and sulphur concentration (LSC). These samples were oven-dried at 60 °C, ground, and then sent to a commercial laboratory for analysis (Hill Laboratories, Hamilton, New Zealand). Because leaf nutrient concentrations can vary along resource availability gradients, individual samples from each fertiliser level were used for the six species which together accounted for more than 80% of total cover among all plots (Garnier et al., 2007). Field-measured traits were measured on all vascular plant species found in all experimental plots in November 2007, just prior to the start of the annual grazing treatments.

A previous study (Chapter 4) had shown that plant species from this study were predominantly differentiated along a nutrient acquisition-conservation trade-off axis corresponding to the "leaf economics spectrum" (Wright et al., 2004), and that community-weighted means (*sensu* Garnier et al., 2004; Díaz et al., 2007a) of leaf traits associated with this axis strongly responded to the long-term manipulations of resource availability and grazing intensity. The analyses focused on community-weighted means of two leaf traits as markers of functional composition: specific leaf area (SLA) and leaf C:N ratio. These two response traits are expected to also act as effect traits by influencing ecosystem processes (Lavorel and Garnier, 2002; Garnier et al., 2004; Quétier et al., 2007b; Díaz et al., 2007a). While leaf traits do not directly capture belowground strategies (De Deyn et al., 2008), previous work in grasslands of varying fertility within the study area showed consistent coupling between leaf and root morphological and chemical traits (Craine and Lee, 2003), suggesting that these leaf traits may act as proxies for belowground strategies.

Plant functional diversity was estimated using SLA, LDMC, LNC, LSC, and LPC, whereas leaf C:N, C:P, and C:S ratios were used to explore potential effects of chemical diversity on litter decomposition (Epps et al., 2007;

Meier and Bowman, 2008; Gessner et al., 2010). In both cases, functional dispersion was used as the abundance-weighted functional diversity index, which is simply the multivariate analogue of the weighted mean absolute deviation (Chapter 2). Functional diversity metrics were computed using the `FD` package (Laliberté and Shipley, 2010) in the R environment (R Development Core Team, 2010).

5.3.5 Aboveground Net Primary Production

Aboveground net primary production (ANPP) was estimated during an 18-month period (October 2007–April 2009), using periodic measurements of live standing plant biomass with a capacitance probe (GrassMaster II, Novel Ways, Hamilton, New Zealand) that was calibrated against oven-dried live biomass harvests from 100 circular quadrats taken across all plots in October 2007 ($R^2 = 0.737$, $P < 0.0001$). Each sampling event consisted of 100 capacitance probe measurements per plot (evenly spread across four longitudinal transects), which were then used to estimate the mean live standing biomass. Capacitance probe measurements were always made directly prior to and after each grazing event in each plot, thus allowing us to quantify the amount of primary production consumed (or trampled) by sheep over that period. In addition, periodic routine measurements (about once a month) were made in between grazing events. Measurements were made when vegetation was dry to prevent overestimation of plant live biomass. All increases in live biomass between two consecutive measurements were summed over the entire sampling period to calculate ANPP (Lauenroth, 2000).

This approach for measuring ANPP avoids the two major methodological problems that have previously complicated the study of grazing impacts on ANPP in grazing systems (McNaughton et al., 1996), and the importance of compensatory plant growth (McNaughton, 1983) in particular. These problems are that (i) grazing animals must be able to remove vegetation biomass during the period of estimation, and that (ii) consumption by grazing animals must be quantified and taken into account (McNaughton et al., 1996). ANPP values are reported as Mg dry matter (DM) ha^{-1} for the entire 18-month sampling period (October 2007–April 2009).

5.3.6 Belowground Net Primary Production

Belowground net primary production (BNPP) was measured using root ingrowth cores (Neill, 1992). Four 8-cm diameter × 30-cm deep soil cores per plot (randomly positioned along a central longitudinal transect) were taken out in October 2007. The resulting holes were immediately filled with root-free soil (i.e., sieved soil taken in an area directly adjacent to the experiment) enclosed in 1-mm mesh nylon bags. Root cores were retrieved in May 2008, cut into three sections corresponding to three depths (0–10 cm, 10–20 cm, and 20–30 cm) and each section was washed through a 1-mm sieve to separate soil from roots, which were then oven-dried and weighed. The same procedure, again with four root ingrowth cores per plot, was repeated for the July 2008–April 2009 period. For each harvested root ingrowth core, all three depth sections were summed, and then averaged values from all four cores per plot for each sampling period. Finally, values from the two sampling periods were summed and expressed as Mg DM ha^{-1} (0–30 cm depth) for the entire 18-month sampling period (October 2007–April 2009), the same period that was used to measure ANPP.

5.3.7 Litter Decomposition

Litter decomposition rate was estimated following a standardised procedure (Garnier et al., 2007). In each plot, freshly senesced plant litter was collected in March 2008 from 10 1×1-m quadrats randomly positioned along a central longitudinal transect. Live biomass, obvious seeds, sheep feces and highly decomposed material were discarded. Litter was air-dried for two weeks, cut into ∼ 5-cm segments, and mixed to yield a "community litter" (Aerts et al., 2003). A standard litter material (cellulose filter paper) was also air-dried and used as a control. Nylon litter bags (1×1-mm mesh size) were filled with ∼ 2-g portions of dry litter or cellulose filter paper. Litter and cellulose filter paper sub-samples (10 per plot) were oven-dried for air-dry weight to oven-dry weight conversions.

Litter was field-incubated back into the plots from where it came. Live plants and stubble were cut to soil surface with a spade in four randomly positioned areas along a central longitudinal transect, within which litter

bags were incubated. Four litter bags per plot, harvest date (after 1, 3, 6, 12, and 18 months of incubation), and litter type (community litter or standard litter) were used, for a total of 40 litter bags per plot (1280 bags in total, counting the two control plots). Rabbit fencing was fixed on top of the litter bags to ensure good contact with the soil and to prevent bags from being blown away by the wind. Litter bags were also enclosed within small ($\sim$ 30 cm radius) sheep exclosures to prevent them from being trampled and damaged. Bags were checked periodically to remove any live plant ingrowth (mostly grass and clover leaves, which were carefully removed). At each harvest date, four bags per litter type were collected from each plot, oven-dried, and weighed.

In addition to incubation within experimental plots, community litter was also decomposed under standard conditions in a homogeneous section of the study site, in order to assess the effects of litter quality alone. Four litter bags (i.e., replicates) per plot and harvest date (1, 3, 6, 12, and 18 months of incubation) were used. The same procedure as described above was used for installation and maintenance. Four controls (cellulose filter paper) per harvest date were also used, for a total of 660 bags.

The negative exponential single-pool decomposition model (Olson, 1963) was used to estimate both the litter decomposition rates k_{plot} (litter incubation within plots) and k_{stand} (litter incubation in standard soil conditions):

$$X(t) = \frac{M(t)}{M(0)}\, e^{-kt}$$

where k is the litter decomposition rate, $X(t)$ is the proportion of litter mass remaining at time t (in days), $M(t)$ is the litter mass remaining at time t, and $M(0)$ is the initial litter mass. By definition, $X(t)$ is in theory bounded between 0 and 1, although in practice values > 1 sometimes occur. The litter decomposition rates $\hat{k}$ were estimated via maximum likelihood ($n = 20$ for each of the 60 plot/incubation type combinations) on untransformed data, using the `bbmle` package (Bolker, 2010) in the R environment (R Development Core Team, 2010).

Nonlinear regression on untransformed data with normal errors has recently been recommended for estimating decomposition rates in single-pool

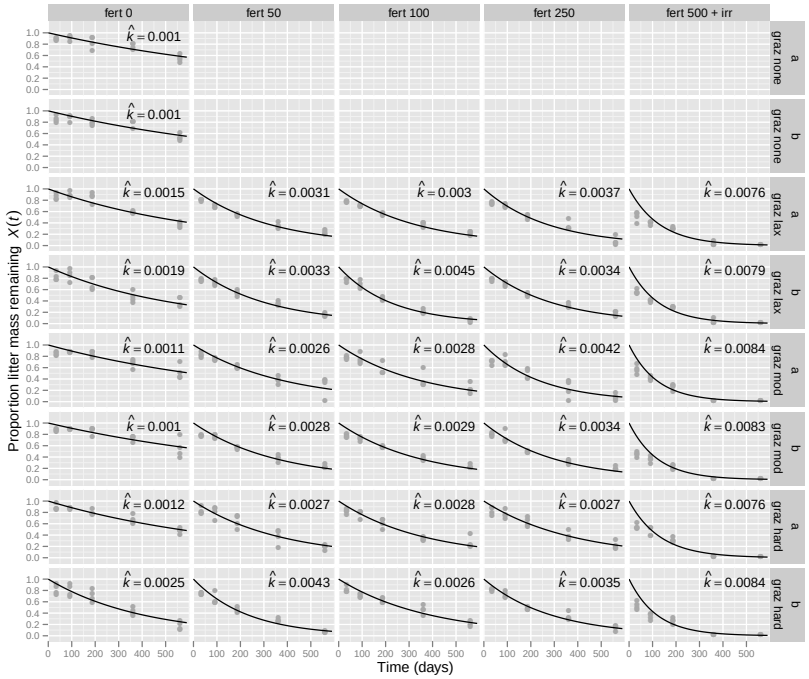

Figure 5.1: Litter decomposition curves for the within-plot incubation experiment (560 days). Each panel represents a particular plot. Columns represent the five fertiliser/irrigation treatments, while rows represent the grazing intensity treatments and replicates (a and b). The two upper panels are from two control plots from an area directly adjacent to the experiment, and which had not been over-sown, fertilised, irrigated, and had not been grazed since at least 1981, and only lightly grazed before then. $\hat{k}$ are estimated litter decomposition rates. $n = 20$ in each panel.

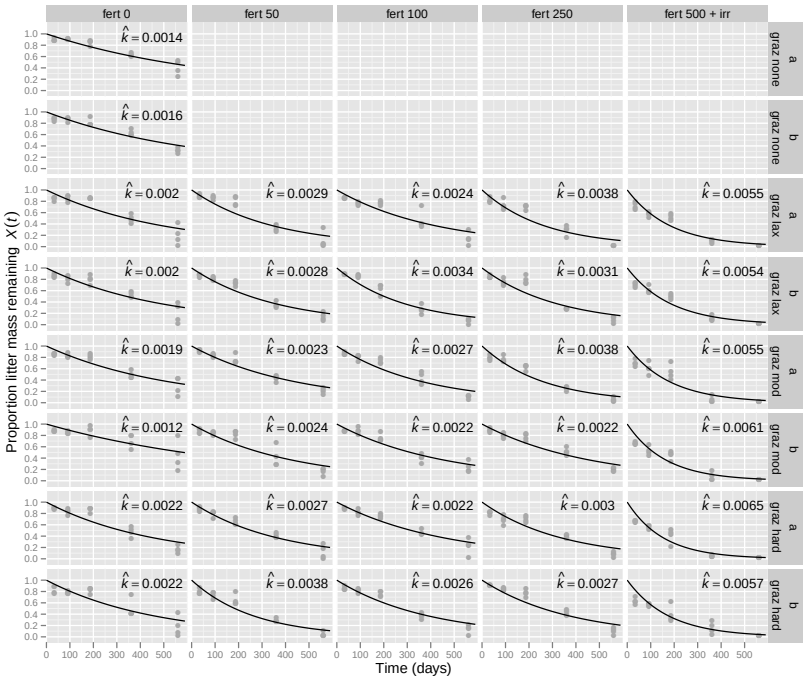

Figure 5.2: Litter decomposition curves for the standard-soil incubation experiment (560 days). See Figure 5.1 for details.

models (Adair et al., 2010). However, the beta distribution can provide a better alternative for modelling proportional bounded data, which often show reduced variance near the bounds (Smithson and Verkuilen, 2006). Thus, models were fitted with either normal or beta errors and selected the best one based on $\Delta\mathrm{AIC_c}$. Because the beta distribution only allows values from the open unit interval $0 < y < 1$, whenever a value > 1 was found, those data were first compressed to the closed unit interval $[0, 1]$ by taking $y' = y/a$, where a is the maximum y value, and then compressing the range to the open unit interval $]0, 1[$ by taking $y'' = [y'(N - 1) + 0.5]/N$, where N is the number of data points (Smithson and Verkuilen, 2006). This transformation was only needed for 24 out of 60 litter decomposition estimates and had very little effect on the data (results not shown). Decomposition curves per plot for each of the two incubation methods are shown in Figures 5.1–5.2.

Because the cellulose filter paper controls decomposed very little during the incubation period in all plots (results not shown), only the community

litter decomposition rates k_{plot} and k_{stand} were used for further statistical analyses.

5.3.8 Soil Respiration

Soil respiration was measured on three occasions during the December 2008–March 2009 period, each time a few days after a rain event, to ensure that the soil was moist. A soil respiration chamber (SRC-1, PP Systems, Hertfordshire, UK) was tightly fitted on each of four PVC collars per plot (pre-installed 6 months before the first measurement) that were inserted into the soil at a depth of 10 cm and randomly positioned along a central longitudinal transect. The soil respiration chamber was left running for 120 seconds on each collar, and a quadratic fit was used to estimate C fluxes from the soil (g C m^{-2} h^{-1}). Vegetation was cut to 2-cm height prior to measurement. Soil temperature at 5-cm depth was measured next to each PVC collar at the time of each soil respiration measurement. At each date, all measurements were taken within a four-hour period from 12:00 to 16:00. Averages of the three measurement rounds were used in the analyses.

5.3.9 Soil Properties

In each plot, four soil samples for each of two depths (0–20 cm and 60–80 cm) were collected from random locations along a central longitudinal transect (September 2008). A composite soil sample per depth was created from these four samples, and these samples were sent to a commercial laboratory (Hill Laboratories, Hamilton, New Zealand) for analysis of: Olsen P, available SO_4, total and available N, organic matter, total C (%C), pH, and bulk density (BD). Total C data were corrected with bulk density data to estimate soil C storage (SC), and results are reported as Mg C ha^{-1} (for 0–20 cm and 60–80 cm depths):

$$\mathrm{SC}_{0\text{–}20\,\mathrm{cm}} = 20 \times \%\mathrm{C}_{0\text{–}20\,\mathrm{cm}} \times \mathrm{BD}$$

$$\mathrm{SC}_{60\text{–}80\,\mathrm{cm}} = 20 \times \%\mathrm{C}_{60\text{–}80\,\mathrm{cm}} \times \mathrm{BD}$$

Samples were also analysed in the laboratory for dissolved organic matter

(DOM), more specifically dissolved organic C and N. To do so, the water-extractable organic matter fraction was extracted by shaking the soil with 10 mM $CaCl_2$ in an overhead shaker (110 rpm, 15 min) at room temperature (∼20°C) with a 1:2 soil:extractant ratio (w/w). The extracts were then centrifuged (15 min, 4500 rpm) and filtered through 0.45 µm cellulose nitrate syringe filters. This method reflects the *in situ* conditions of the soil solution (Zsolnay, 2003).

Previous work has reported on differences in soil nutrient pools and fluxes and organic matter components among the different experimental treatments for years 10–15 of the experiment (Scott, 2000b,d,e).

5.3.10 Statistical Analyses

Differences among Experimental Treatments

Linear mixed models with random intercepts per block and whole plot were used whenever testing for differences among experimental treatments for a given variable, thus taking into account the hierarchical (i.e., split-plot) structure of the experimental design. Analyses were done using the `nlme` (Pinheiro et al., 2010), `multcomp` (Hothorn et al., 2008), and base packages in the R environment (R Development Core Team, 2010). Residuals were inspected to verify model assumptions. When heterogeneity was detected, an appropriate variance structure was specified (Pinheiro and Bates, 2000), using the top-down approach described by Zuur et al. (2009). Model selection on the fixed component of the model (i.e., the main effects of fertiliser, grazing intensity and their interaction) was based on minimising the Akaike Information Criterion (AIC) and using likelihood ratio tests on models fitted via maximum likelihood estimation. The final model was fit by restricted maximum likelihood estimation (REML). *Post hoc* Tukey pairwise multiple comparisons were used to test for differences among treatment levels (Hothorn et al., 2008).

Multilevel Causal Path Models

Generalised multilevel path models (Shipley, 2009a) were used to test different causal hypotheses involving soil resource availability and grazing in-

tensity, plant functional composition and diversity, and ecosystem processes. Standard structural equation modelling (SEM) approaches based on comparisons between observed and predicted covariance matrices could not be used because the hierarchical nature of the experimental design violated the assumption of independence among observations. Besides allowing us to consider the hierarchical nature of the design, another benefit of generalised multilevel path models is that they offer a flexible way to take into account non-linear relationships and interactions among variables (Shipley, 2009a).

Testing the validity of a generalised multilevel causal path model consists of: (i) finding the "basis set" $\mathbf{B}_{\mathrm{U}}$ of independence claims implied by a directed acyclic causal graph (i.e., a box-and-arrow causal diagram that involves no feedback loops) that, together, expresses the full set of dependence and independence claims implied by the causal graph; (ii) obtaining the probability p_i associated with each the k independence claims in $\mathbf{B}_{\mathrm{U}}$, using appropriate statistical tests (in this case, linear mixed models, as described above); (iii) combining the p_i using $C = -2\sum_{i=1}^{k} \ln(p_i)$; and (iv) comparing the C statistic to a chi-square (χ^2) distribution with $2k$ degrees of freedom (Shipley, 2009a). A causal model can be rejected if the P-value associated with its C statistic is smaller than the specified α-level (here, $\alpha = 0.05$), since a significant P-value implies that the data depart significantly from what would be expected under such a causal model (Shipley, 2009a).

When analysing experimental data under an SEM framework, categorical variables corresponding to experimental treatments can be dealt with in several ways (Grace, 2006). Because the levels for both experimental treatments were ordered (corresponding to five increasing levels of soil resource availability [i.e., P/S fertiliser and irrigation] and sheep relative grazing intensity [i.e., 2:3:4 sheep stocking ratios]), it was possible to adopt the typical approach of converting them to ranks, effectively treating the design as a response-surface design (Grace, 2006). While the fertiliser/irrigation treatment was treated in that way (resulting in a continuous variable from 1 to 5 which is referred to as "soil resource availability"), this approach was not used for the grazing intensity treatment. The rationale was that while it is relatively easy to control the amount of P/S fertiliser and water added to plots each year (and thus to assume fixed values for the soil resource availability index), manipu-

lating ∼150 sheep in an experimental setting is inherently more challenging. Although sheep numbers were fixed according to the 2:3:4 ratio within each whole plot for each grazing event, as defined by the experimental design, it is not possible to control sheep foraging behaviour and thus it is difficult to accurately determine whether the amount of plant biomass consumed actually corresponds to the targeted 2:3:4 ratio or whether it is varies non-linearly in a density-dependent manner. Moreover, the fertiliser/irrigation treatment led to large shifts in plant taxonomic and functional composition (Chapters 3 and 4; Scott, 2007) and levels of primary production (Fig. 5.4a). This heterogeneity in vegetation composition among resource availability levels makes it difficult to estimate with certainty whether the levels of remaining plant biomass in the moderate grazing treatments after a grazing event (which determines the duration of the grazing event in all three grazing intensity subplots within a whole plot, and thus the relative amount of plant biomass consumed in these three subplots) are actually comparable across the different whole plots.

As a solution to these problems, an appropriate and meaningful measure of grazing intensity in grasslands is simply the proportion of ANPP grazed by animals (e.g., Bagchi and Ritchie, 2010). Because the sampling methodology used to estimate ANPP gave a direct estimate of the amount of plant biomass consumed (or trampled) by sheep, the ratio of grazed ANPP over total ANPP for the October 2007–April 2009 period was used as the measure of grazing intensity in generalised multilevel path models. This yields a direct estimate of grazing intensity that is comparable across plots and thus avoids the aforementioned methodological problems associated with treating grazing intensity as a ranked variable based on the levels of the grazing intensity experimental treatment. Grazing intensity values above one (i.e., more plant biomass was grazed than produced during the measurement period) are possible because the measurement period for ANPP started near peak standing biomass in October 2007 but ended in April 2009, directly after all plots were grazed before the winter resting period.

While soil resource availability and grazing intensity would be orthogonal to each other had they both been treated as ranked variables (by virtue of the experimental design), the fraction of total ANPP grazed increased in a

non-linear fashion with soil resource availability ($R^2 = 0.585$, $P < 0.001$; Fig.). This is consistent with patterns found in natural ecosystems, where ecosystems with higher rates of primary production sustain a greater level of herbivory per unit of primary production (McNaughton et al., 1989). The dependence of grazing intensity on soil resource availability was explicitly considered in all causal path models. An additional linear mixed model that included both soil resource availability and a ranked grazing variable corresponding to the different levels of the grazing intensity treatment showed that both predictors had significant ($P < 0.05$) positive effects on the continuous grazing intensity measure (i.e., the fraction of total ANPP grazed by sheep). Importantly, no significant interaction was detected ($P = 0.303$). Therefore, this shows that despite the fact that greater soil resource availability led to a greater proportion of total ANPP being consumed by sheep, increasing levels of the grazing intensity experimental treatment still led to greater herbage consumption once this effect of soil resource availability was accounted for.

Linear mixed models with random intercepts per block and whole plot were used to test the k independence claims implied by each causal path model, allowing us to take into account the hierarchical nature of the experiment (Shipley, 2009a). Data on ecosystem processes (ANPP, BNPP, litter decomposition, and soil respiration) were log-transformed to linearise relationships (see Fig. 5.4). All predictors were centred on their means (i.e., subtracting the mean) to facilitate interpretation and to avoid multicollinearity problems due to the inclusion of interactions and polynomials (Aiken and West, 1991). Residuals were inspected to verify model assumptions and appropriate variance structures were used in the presence of heterogeneity (Pinheiro and Bates, 2000).

Three potentially important interactions between predictors were considered in the models, based on expectations derived from previous work. Because the effect of diversity on ecosystem functioning can vary with soil resource availability (Fridley, 2002), a soil resource availability $\times$ functional (and chemical) diversity interaction was included whenever appropriate. Moreover, because diversity effects on ecosystem functioning can become less important under greater disturbance intensity (Cardinale et al., 2000), an interaction involving grazing intensity and functional (and chemical) diversity was

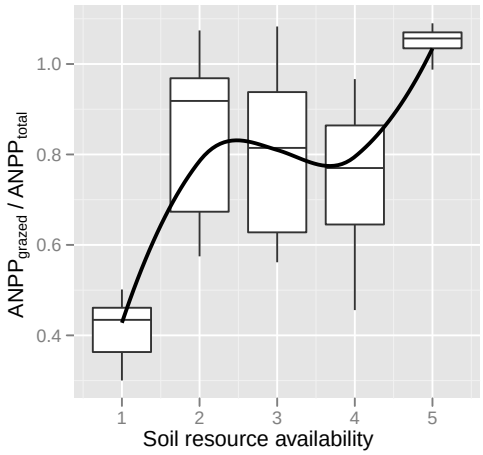

Figure 5.3: Grazing intensity (fraction of ANPP grazed) increased non-linearly with soil resource availability. The relationship was modeled using a linear mixed model, with random intercepts per block and whole plot and with a heterogeneous variance structure for the different levels of the fertiliser treatment. First, second, and third-order polynomials of soil resource availability were used as the fixed predictors ($R^2 = 0.585$, $P < 0.0001$). The black line shows a smoothed loess curve (span = 0.85) through the population fitted values. Soil resource availability was centred prior to analysis but results are reported back in original values to facilitate interpretation.

also included. Finally, a soil resource availability × grazing intensity interaction was considered as a potential influence over plant functional composition, functional diversity, and ecosystem processes, since the strength and direction of herbivore impacts on vegetation and ecosystem processes are thought to depend on soil resource availability (Olff and Ritchie, 1998; Bardgett and Wardle, 2003).

When testing an independence claim for a given predictor, which included interactions involving that predictor (i.e., the independence claim involved more than one fixed term), the null probability p_i was taken from a likelihood ratio test involving nested models with and without the terms of interest, using maximum likelihood estimation. While likelihood ratio tests can be non-conservative when comparing nested models with different fixed effects when sample sizes are small (Pinheiro and Bates, 2000), the consequence of this would not be important in the context of testing the validity a causal path model. Indeed, a less conservative test leading to a smaller P-value would inflate the C statistic, thus increasing the chance of rejecting the causal model and therefore forcing the inclusion of the independence claim as a dependence claim in a second path model. However, because the individual path coefficients in each causal model are ultimately tested for significance using conditional t-tests, which are recommended over likelihood ratio tests for hypothesis tests involving fixed effects (Pinheiro and Bates, 2000), this approach would not overestimate the importance of these paths in the final model.

Polynomials of main terms were used to model non-linear relationships, but only when differences in AIC and results of likelihood ratio tests (using maximum likelihood estimation) provided unequivocal support for their inclusion (i.e., $\Delta\text{AIC} > 8$ and $P < 0.001$ for likelihood ratio tests), again because of the liberal nature of the likelihood ratio test for comparing models with different fixed effects (Pinheiro and Bates, 2000). When testing an independence claim involving a non-linear relationship modeled with multiple polynomials of a predictor, a single composite variable was first created from these polynomial terms by fitting a mixed model with all polynomials as predictors, extracting its regression coefficients (i.e., fixed effects), and then multiplying each polynomial by its regression coefficient and summing them

together into one composite variable (Grace et al., 2007). REML estimation was used and p_i was taken from the P-value associated with the t-statistic for the regression coefficient of the composite variable.

For all causal models, individual path coefficients leading to endogenous variables (i.e., variables with arrows leading to them) were fitted using REML and tested for significance (Shipley, 2009a). Again, residuals were inspected to verify model assumptions, and appropriate variance structures were used in the presence of heterogeneity (Pinheiro and Bates, 2000). Significance of individual path coefficients was assessed using conditional t-tests (Pinheiro and Bates, 2000).

Model fits for endogenous variables were assessed via an R^2 statistic developed specifically for linear mixed models (Kramer, 2005). While the calculation and interpretation of R^2 statistics for mixed models are still under debate, and such statistics cannot be interpreted in the same way as their least squares counterpart (Edwards et al., 2008), this R^2 statistic was simply used as an overall measure of fit for the different models. Because the final models used REML estimation, and this R^2 measure used relies on maximum likelihood estimation (Kramer, 2005; Edwards et al., 2008), these R^2 statistics should be interpreted with caution. Nevertheless, they should still give a reasonable absolute indication (rather than a comparative measure such as AIC) of how well or poorly a particular model fits the data.

Because all predictors were centred, unstandardised path coefficients can be interpreted as the amount of change in the response variable following a unit change in the predictor when all other predictors are held constant at their mean values (Aiken and West, 1991). However, in the presence of an interaction this interpretation is no longer valid; in that case, the unstandardised path coefficient for a predictor involved in the interaction is interpreted as its average effect on the response variable when the conditioning variable (i.e., the other predictor involved in the interaction) is held at its mean value (Aiken and West, 1991). The unstandardised path coefficient for the interaction, on the other hand, represents the amount of change in the slope of the regression of the response variable on one of the predictors involved in the interaction, following a one-unit change in the other predictor (Aiken and West, 1991).

Standardised coefficients for main terms and interactions were computed as described by Aiken and West (1991), whereas those for non-linear relationships involving polynomials were computed from composite variables of the polynomial terms (Grace et al., 2007). Only standardised coefficients are meaningful in the latter case (Grace et al., 2007). Contrary to unstandardised coefficients, standardised coefficients can be directly compared to each other and represent the relative importance of each path. These standardised coefficients are interpreted in a similar way as unstandardised coefficients, except that changes in both predictors and response variables are expressed in standard deviation units.

Causal models with significant C statistics ($P < 0.05$) were promptly rejected. For each set of models, the best and most parsimonious causal model were selected among a set of competing models by choosing the one that agreed with the data ($P > 0.05$) but did not contain irrelevant paths, i.e., paths that were not significant and could be removed without decreasing the C/df ratio (Jöreskog, 1969). The only exception to this rule was when an interaction involving two terms was significant but one of the main effects was not. In that case, both main terms had to be included in the model to satisfy the principle of marginality (Venables and Ripley, 2002). All of the aforementioned analyses were conducted using the `nlme` (Pinheiro et al., 2010) package in the R environment (R Development Core Team, 2010).

5.4 Results and Discussion

Soil resource availability had strong cascading effects on ecosystem functioning (Fig. 5.6), with direct positive effects on ANPP and litter decomposition being likely caused by greater plant resource uptake and stimulated microbial activity (Lambers et al., 2008a). Moreover, soil resources drove changes in traits of the dominant species, as predicted (Grime, 2002; Lavorel and Garnier, 2002; Garnier et al., 2004; Díaz et al., 2007a; Quétier et al., 2007b); SLA increased sharply from the lowest to the second lowest soil resource availability level, but then varied little with further increases in resource availability (Fig. 5.5), whereas leaf C:N showed the opposite trend (Fig. 5.7). Because these traits are tightly linked to the leaf economics spectrum (Wright et al.,

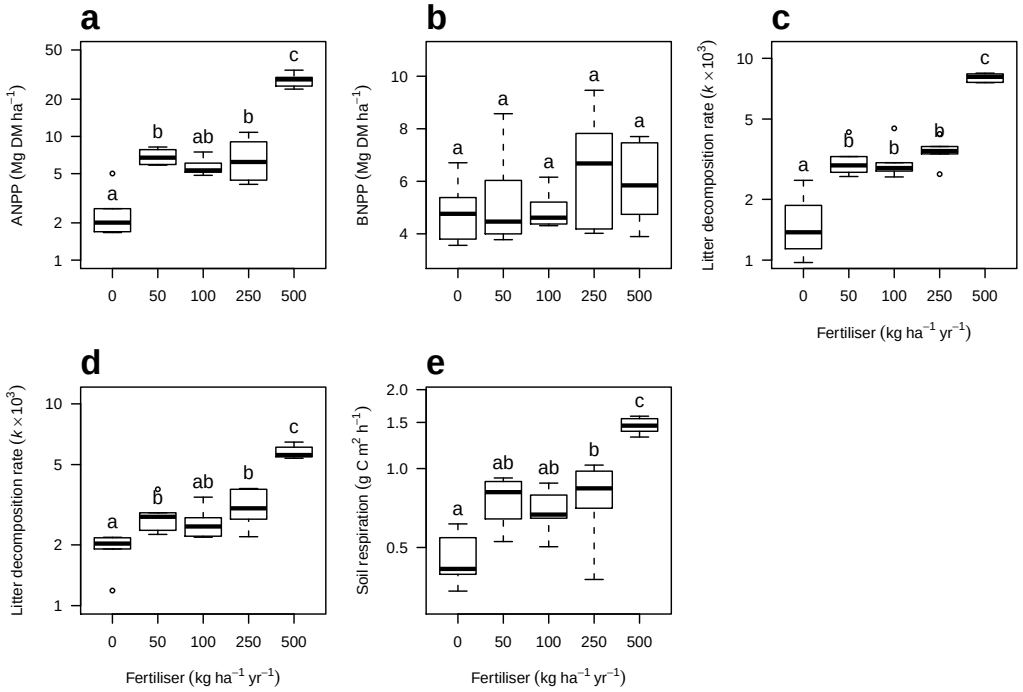

Figure 5.4: Differences in ecosystem processes among fertiliser levels. (**a**) ANPP, (**b**) BNPP, (**c**) litter decomposition (incubation within plots), (**d**) litter decomposition (incubation under standard soil conditions), and (**e**) soil respiration. Different letters indicate significant ($P < 0.05$) differences following *post hoc* Tukey tests. The central bar shows the median, the box represents the interquartile range (IQR), the whiskers show the location of the most extreme data points still within 1.5 +/− the upper or lower quartiles, and small open circles are outliers. All panels except (**b**) have their y-axes on logarithmic scales.

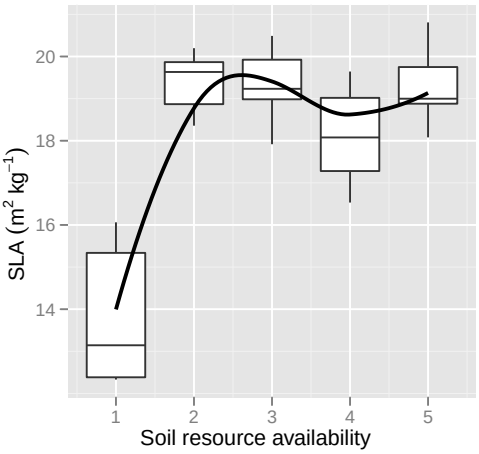

Figure 5.5: Community-weighted specific leaf area (SLA) increased non-linearly with soil resource availability. First, second, and third-order polynomials of soil resource availability were used as the fixed predictors (R^2 = 0.535, $P < 0.0001$). The black line shows a smoothed loess curve (span = 1.1) through the population fitted values. Soil resource availability was centred prior to analysis but results are reported back in original values to facilitate interpretation.

2004) and correlate with leaf lifespan (Reich et al., 1992), these results support the view that leaf attributes that reduce nutrient losses hold a long-term advantage under nutrient limitation, whereas those associated with a rapid growth rate become dominant under high fertility (Chapin, 1980; Lambers and Poorter, 1992; Herms and Mattson, 1992; Aerts, 1995; Reich et al., 1997; Aerts and Chapin, 2000; Grime, 2002). On the other hand, higher grazing intensity decreased leaf C:N (Fig. 5.6b), suggesting the emergence of a grazing-resistant strategy, which is expected under the episodic but hard grazing (Rosenthal and Kotanen, 1994) to which experimental plots were subjected. These plant trait shifts in turn directly increased ANPP and litter decomposition (Fig. 5.6), as SLA is an important component of plant relative growth rate (Poorter and Remkes, 1990; Garnier, 1992; Lambers et al., 2008a), whereas leaf C:N is a good indicator of litter quality for herbaceous species (Lambers et al., 2008a).

The primacy of soil resource availability was also demonstrated through its moderating influence on the strength and direction of herbivore-mediated

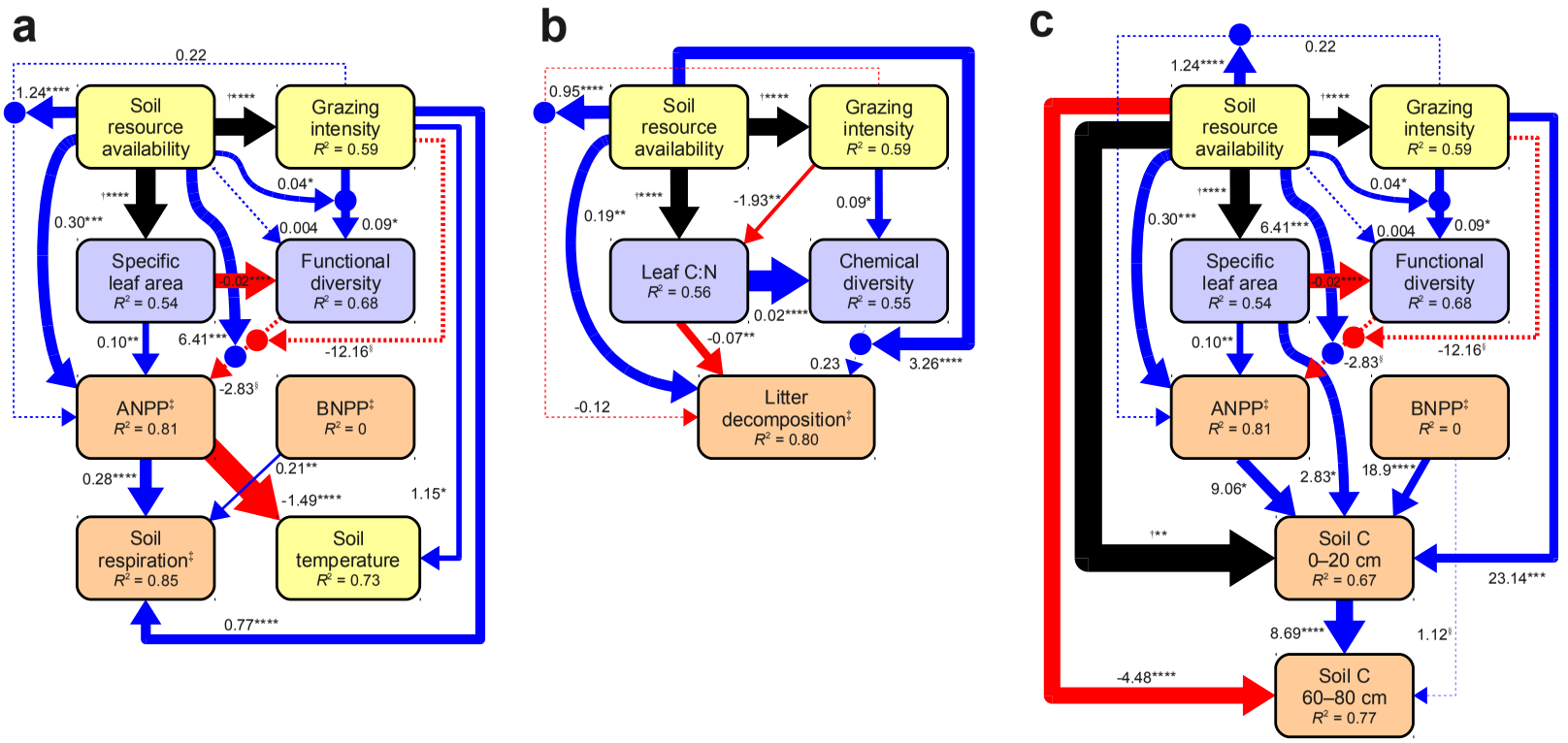

Figure 5.6: Best-fitting causal path models for (**a**) ANPP, BNPP, and soil respiration, (**b**) litter decomposition, and (**c**) soil carbon sequestration. All causal models fitted the data well (**a**: $\chi^2 = 20.4$, $df = 28$, $P = 0.851$; **b**: $\chi^2 = 2.46$, $df = 2$, $P = 0.293$; **c**: $\chi^2 = 20.7$, $df = 22$, $P = 0.541$). Arrows represent the flow of causality. Blue arrows indicate positive effects, while red arrows indicate negative effects. Black arrows are non-linear relationships. Arrows leading to other arrows represent interactive effects. Path coefficients are unstandardised partial regression coefficients. Arrow widths are proportional to the standardised path coefficients. Dotted arrows represent non-significant ($P > 0.05$) relationships. †No unstandardised path coefficients are available for non-linear relationships. ‡Log-transformed. §$0.05 < P < 0.1$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ****$P < 0.0001$.

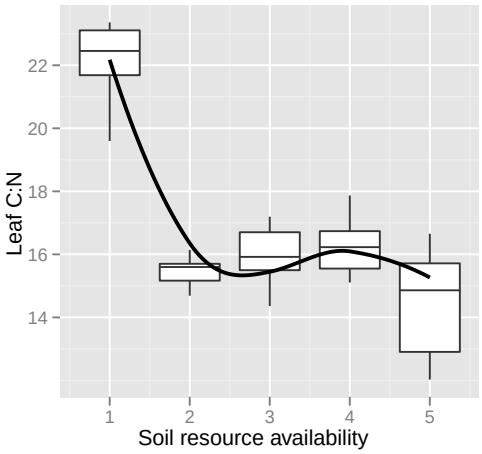

Figure 5.7: Community-weighted leaf C:N ratio decreased non-linearly with soil resource availability. First, second, and third-order polynomials of soil resource availability, as well as grazing intensity were used as the fixed predictors ($R^2 = 0.644$), and all terms were significant ($P < 0.05$). See Figure 5.5 for details.

impacts on ecosystem processes. Strikingly, impacts of grazing intensity on ANPP and litter decomposition shifted from negative to positive with increasing soil resources (Figs. 5.6a–b and 5.8b–c). The tenet that impacts of grazing by large herbivores depend on soil resource availability has been hypothesised (Bardgett and Wardle, 2003) and supported by field studies along natural resource gradients (Augustine and McNaughton, 2007), yet until now strong experimental tests have remained elusive.

Besides physical disturbance, grazing can impact ecosystem processes through changes in the quantity and quality of resources returned to the soil (McNaughton et al., 1997; Bardgett and Wardle, 2003), which in the longer term may be due to shifts in plant functional composition (Pastor et al., 1988; Bardgett and Wardle, 2003; Bagchi and Ritchie, 2010). In accordance with this mechanism, grazing intensity directly decreased leaf C:N, which in turn increased litter decomposition (Fig. 5.6b). However, this could not explain the strong interaction between the effects of soil resource availability and grazing intensity observed for both ANPP and litter decomposition. When litter decomposition rate was measured under standard soil conditions, this

interaction disappeared (Fig. 5.9). This suggests that this interactive effect was mediated through aboveground-belowground feedbacks, and not through more pronounced herbivore-induced increases in plant secondary compounds under lower resource availability (Coley et al., 1985), which could have reduced litter decomposition rate (Findlay et al., 1996) and ultimately, nutrient cycling and ANPP. Although the nature of these aboveground-belowground feedbacks remain to be elucidated, one such feedback pathway could be that under greater soil resource availability, increases in root exudation through grazing-induced defoliation stimulated microbial decomposition and nitrogen mineralisation (Hamilton and Frank, 2001; Hamilton et al., 2008), thus promoting litter decomposition and ANPP. Conversely, under low soil resource availability, such beneficial effects of grazing may be outweighed by other detrimental impacts. For example, grazing can reduce the abundance and activity of litter-consuming arthropods (Hutchinson and King, 1980), potentially restricting litter decomposition. Moreover, mycorrhizal associations play significant roles in plant mineral nutrition under low soil fertility (Lambers et al., 2008a,b), and grazing has adverse effects on these associations through photosynthate limitation (Gehring and Whitham, 1994).

Changes in plant functional composition towards a more rapid-growth strategy led to strong reductions in functional diversity and chemical diversity (Fig. 5.6). This may be due to shifts in competition intensity, whereby the coexistence of alternative plant strategies of approximately equal fitness is promoted in communities dominated by slow-growing plants, whereas dominance by fast-growing plants leads to the competitive exclusion of those with inherently slower growth (Grime, 1973, see also Chapter 4). In contrast, grazing intensity increased functional and chemical diversity, although for functional diversity the effect of grazing became more positive as resource availability increased. This may be because higher grazing intensity suppresses competitive dominance, and this effect of grazing may become more important when soil resources are plentiful and opportunities for competitive exclusion are greatest (Grime, 1973).

Functional diversity is expected to provide a stronger mechanistic link than measures of species diversity with regard to positive effects of biodiversity on ecosystem functioning (Díaz and Cabido, 2001; Tilman, 2001; Naeem

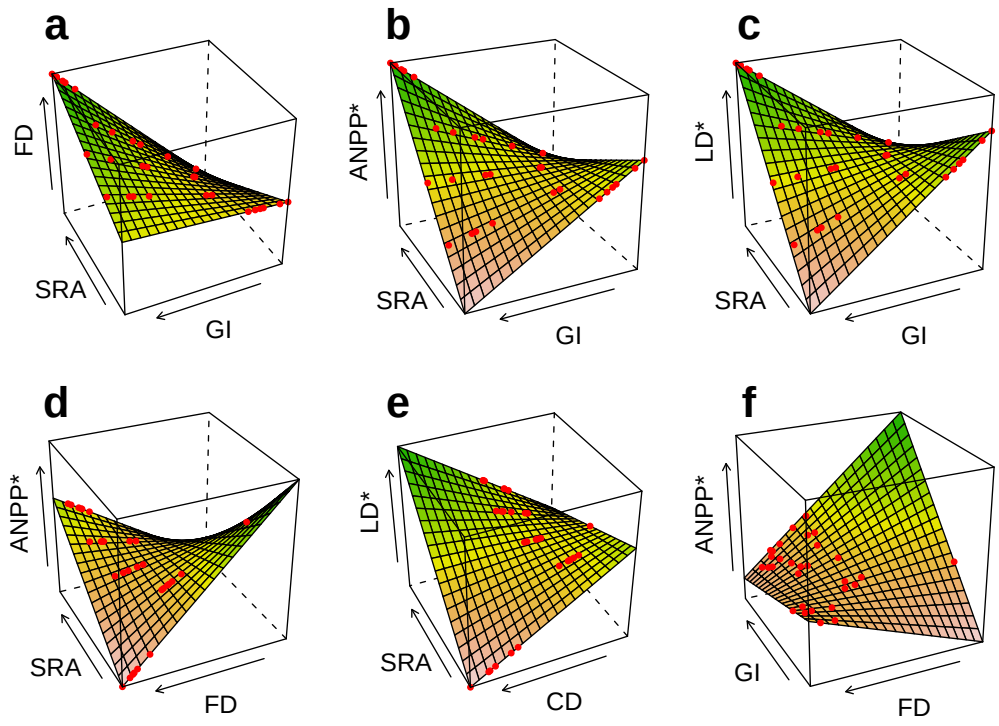

Figure 5.8: Interactive effects on functional diversity, ANPP, and litter decomposition. In each panel, the surface represents the population fitted values for the two terms involved in the interaction, holding all other fixed terms in the model constant at their mean values. Arrows indicate increasing values. The ranges of the x- and y-axes were determined from the range of the data. Red dots show the population fitted values associated with individual plots. *Log-transformed. Codes for variables are defined in Table 5.1.

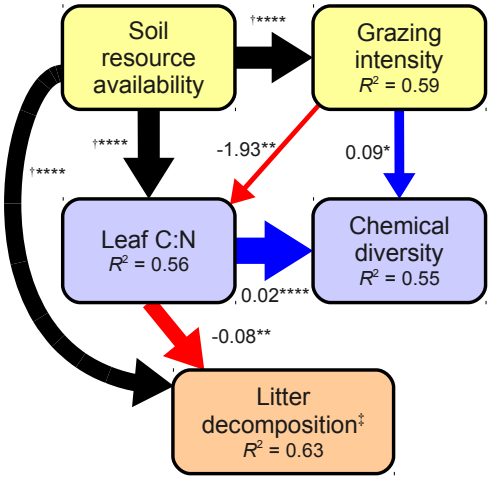

Figure 5.9: Best-fitting multilevel causal path model for litter decomposition under standard soil conditions. The causal model was supported by the data ($\chi^2 = 7.43$, $df = 6$, $P = 0.291$). †Nonlinear relationships. ‡Log-transformed. §$0.05 < P < 0.1$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ****$P < 0.0001$. See Figure 5.6 for details.

and Wright, 2003; Hooper et al., 2005; Díaz et al., 2007b). Yet surprisingly, higher plant functional and chemical diversity were associated with lower ANPP and litter decomposition at the lowest soil resource availability level (Fig. 5.8d–e), where both native and total species richness were greatest (see Chapter 4). Nevertheless, effects of functional and chemical diversity on ANPP and litter decomposition became increasingly positive under greater soil resource availability (Fig. 5.8d–e). These results, in accordance with those from a short-term grassland experiment (Fridley, 2002), again highlight the importance of soil resources, and suggest that complementary resource use may only become important when resources are plentiful.

In contrast to ANPP, belowground net primary production (BNPP) was not influenced by soil resource availability, grazing intensity, plant traits or functional diversity, and it varied independently of ANPP (Fig. 5.6a). The unresponsiveness of BNPP to changes in soil resource availability may have arisen because plants generally allocate a greater proportion of their resources to root growth under lower soil resource availability, in order to match above-ground demands (Lambers et al., 2008a). The absence of impacts of grazing

accords with previous findings (McNaughton et al., 1998). Despite previous work in the study area showing consistent coupling between leaf and root traits (Craine and Lee, 2003), SLA did not explain variation in BNPP. Because measuring root traits can be challenging, identifying easily-measurable aboveground traits that capture belowground processes is an important area for future research (De Deyn et al., 2008).

Soil resource availability, grazing intensity and their associated impacts on plant traits and functional diversity had cascading effects on soil respiration via their effects on ANPP (Fig. 5.6a). While soil temperature can moderate soil respiration, and was thus measured as an additional covariate, it did not explain any additional variation (Fig. 5.6a), possibly due to thermal acclimation of plant respiration (Atkin and Tjoelker, 2003). The dominant influence of ANPP on soil respiration (Fig. 5.6) is in line with previous work (Tavares Corrêa Dias et al., 2010) and presumably reflects the large root respiratory costs associated with ion transport (Lambers et al., 2008a), and larger carbon inputs available for heterotrophic respiration (Raich and Tufekciogul, 2000). In addition, BNPP had a positive effect on soil respiration (Fig. 5.6), most likely reflecting root growth respiration (Lambers et al., 2008a). Conversely, the strong positive effect of grazing intensity (Fig. 5.6) may be due to microbial stimulation of organic matter mineralisation, possibly from dung and urine return (McNaughton et al., 1997; Bardgett and Wardle, 2003) or defoliation-induced increases in root exudation (Hamilton and Frank, 2001; Hamilton et al., 2008). Support for this hypothesis came from higher dissolved organic carbon ($\beta = 70.7$, $t = 3.33$, $P = 0.004$) and dissolved organic nitrogen ($\beta = 3.25$, $t = 2.18$, $P = 0.043$) in the surface soil layer (0–20 cm) under higher grazing intensity, with these effects being consistent across soil resource availability levels (soil resource availability $\times$ grazing intensity interactions, $P = 0.107$ and $P = 0.853$, respectively). Because the soil respiration measurements were point estimates, it is unclear whether these results can be extrapolated to annual soil respiration. Nevertheless, because up to 98% of the total carbon in grasslands can be stored belowground (Jones and Alison, 2004), and soil respiration accounts for most carbon loss from soils (De Deyn et al., 2008), this potential herbivore-mediated positive feedback could have important consequences for the global carbon cycle.

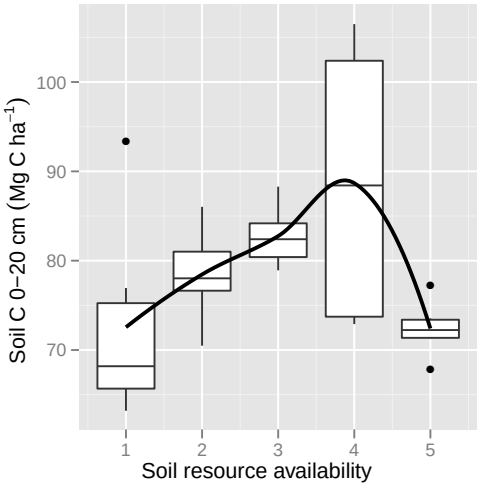

Figure 5.10: Surface soil (0–20 cm depth) carbon shows a non-linear response to soil resource availability. A linear mixed model with random intercepts per block and whole plot was used. Boxplots of population fitted values of the full model are shown. The black line shows a smoothed loess curve (span = 1.1) through these population fitted values. Soil resource availability was centred prior to analysis but results are reported back in original values to facilitate interpretation.

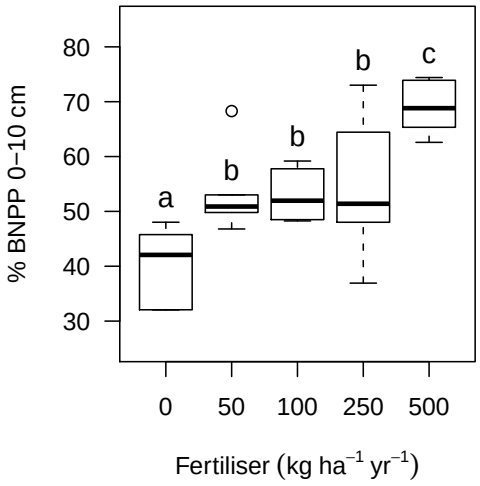

Figure 5.11: Depth distribution of BNPP in 0–10 cm soil layer among fertiliser levels. Percentages express the amount of BNPP in the 0–10 cm soil layer relative to the entire 0–30 cm profile in which BNPP was estimated. Different letters indicate significant ($P < 0.05$) differences following *post hoc* Tukey tests. The central bar shows the median, the box represents the interquartile range (IQR), the whiskers show the location of the most extreme data points still within 1.5 +/− the upper or lower quartiles, and small open circles are outliers.

Long-term manipulation of soil resource availability also had a dominant, non-linear effect on the amount of carbon stored in the soil surface (0–20 cm depth; Fig. 5.6c). Soil carbon increased progressively with fertilisation rate, but then dropped sharply at the highest resource availability level (Fig. 5.10), which was irrigated and sustained by far the greatest ANPP (Fig. 5.4a). A limited rooting depth distribution can restrict opportunities for build-up of soil carbon (De Deyn et al., 2008), and indeed there was a significantly greater proportion of BNPP restricted to the 0–10 cm soil layer at the highest soil resource availability (Fig. 5.11). Moreover, because the study area frequently experiences summer moisture deficits, which can effectively halt soil respiration, irrigation may have promoted soil carbon loss by increasing soil respiration on an annual scale. Thus, increased plant production through high fertilisation and irrigation do not necessarily translate into greater soil carbon sequestration in grasslands (Jones and Alison, 2004).

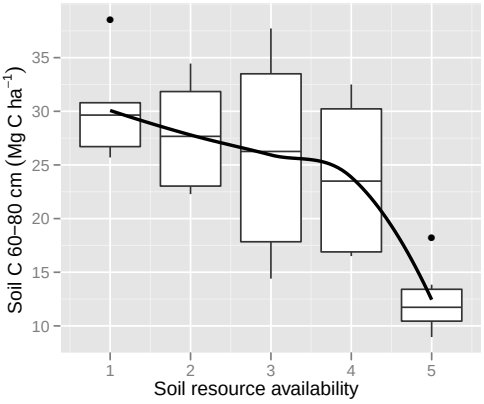

Figure 5.12: Deeper (60–80 cm depth) soil carbon stores decrease with greater soil resource availability. A linear mixed model with random intercepts per block and whole plot was used. Boxplots of population fitted values of the full model are shown. The black line shows a smoothed loess curve (span = 1.1) through these population fitted values. Soil resource availability was centred prior to analysis but results are reported back in original values to facilitate interpretation.

Once this dominant, non-linear effect of soil resource availability was accounted for, both ANPP and BNPP increased soil surface carbon (Fig. 5.6c), presumably through greater plant-derived inputs to the soil (De Deyn et al., 2008). Grazing intensity also had a strong positive effect (Fig. 5.6c), which could occur if stimulation of microbial biomass from defoliation-induced increases in root exudation (Hamilton and Frank, 2001; Hamilton et al., 2008) promotes the formation of soil micro-aggregates by interacting with soil minerals, particularly clay particles (Jones and Alison, 2004; Six et al., 2006; De Deyn et al., 2008). Finally, the positive effect of SLA on surface soil carbon (Fig. 5.6c) may arise because rhizodeposition and fine root turnover tend to be greater for faster-growing species (Ryser and Lambers, 1995; De Deyn et al., 2008), which can in turn enhance soil carbon storage if this also promotes soil micro-aggregates (De Deyn et al., 2008). This shows that a trait-based approach should enhance our understanding of the processes controlling soil carbon storage (De Deyn et al., 2008).

Soil carbon residing at depth provides a more stable carbon pool (Jones and Alison, 2004). Because very few roots were found beyond 40 cm, the

amount of soil carbon stored at greater depth (60–80 cm) is expected to originate mainly through leaching from upper soil layers (Jones and Alison, 2004). Accordingly, it was primarily driven by surface soil carbon (Fig. 5.6c). However, soil resource availability also strongly decreased deeper carbon stores (Figs. 5.6c and 5.12). This may occur if more labile organic matter is returned to the soil under greater resource availability (Wardle et al., 2004; De Deyn et al., 2008), restricting opportunities for recalcitrant organic matter to leach to deeper soil layers. Nevertheless, because the amount of carbon stored in surface soil is much greater than the amount stored at depth in grasslands (Jones and Alison, 2004), these results suggest that an intermediate level of fertilisation may promote soil carbon sequestration in temperate grasslands, echoing previous conclusions (Jones and Alison, 2004; Soussana et al., 2004).

5.5 Conclusions

The results from this long-term experiment show that land-use intensification has cascading effects on ecosystem functioning, both through direct effects of changes to resource availability (Burke et al., 1997; Lambers et al., 2008a) and grazing (McNaughton et al., 1997), and through the indirect effects of these environmental forces on plant traits (Grime, 1998; Chapin et al., 2000; Lavorel and Garnier, 2002; Hooper et al., 2005; Quétier et al., 2007b; Lavorel et al., 2007) and functional diversity (Díaz and Cabido, 2001; Naeem and Wright, 2003; Heemsbergen et al., 2004; Hooper et al., 2005). Not only did soil resource availability have the strongest effect on functioning, but it also moderated the effect of most other drivers. Indeed, this study provides strong experimental evidence that the effects of both functional diversity and herbivores on ecosystem functioning depend on soil resource availability (Fridley, 2002; Bardgett and Wardle, 2003).

Higher functional and chemical diversity, under the lowest soil resource availability level (which also sustained the greatest species richness), were associated with lower ANPP and decomposition rates. This suggests that the link between biodiversity and ecosystem functioning provides a poor argument for conservation (Srivastava and Vellend, 2005), at least in these

grasslands. However, functional diversity can be important for ecosystem functioning, even against the background of other abiotic and biotic drivers (Huston and McBride, 2002; Srivastava and Vellend, 2005), provided there are sufficient soil resources (Fridley, 2002). Therefore, this study support the idea that functionally diverse species mixtures offer a promising avenue for improving the efficiency of production systems, such as intensive pastures (Sanderson et al., 2004, 2007) or biofuel crops on abandoned agricultural land (Fargione et al., 2008).

Grasslands are expected to undergo rapid intensification of grazing pressure and fertiliser use in the coming decades to meet the growing global demand for livestock products (Bouwman et al., 2005). The results from this study suggest that increasing grazing pressure in marginal grasslands can lead to negative feedbacks on ecosystem functioning, potentially compromising long-term production potential. On the other hand, large concomitant increases in agricultural inputs and grazing intensity can lead to positive feedbacks on functioning, yet restrict opportunities for soil carbon sequestration. This study shows how understanding the direct, indirect, and synergistic effects of land-use changes on communities and ecosystems should help us to better assess and balance such inherent trade-offs among multiple ecosystem functions (DeFries et al., 2004; Foley et al., 2005; Carpenter et al., 2006).

Chapter VI

Land-Use Intensification Reduces Functional Redundancy and Response Diversity in Plant Communities[1]

6.1 Summary

Ecosystem resilience depends on functional redundancy (the number of species contributing similarly to an ecosystem function) and response diversity (how functionally similar species respond differently to disturbance). This study explores how land-use change impacts these attributes in plant communities, using data from 18 land-use intensity gradients that represent five biomes and > 2800 species. Functional groups are identified using multivariate analysis of plant traits which influence ecosystem processes. Functional redundancy is calculated as the species richness within each group, and response diversity as the multivariate within-group dispersion in response trait space, using traits that influence responses to disturbances. Meta-analysis across all data sets showed that land-use intensification significantly reduced both functional redundancy and response diversity, although specific relationships varied considerably among the different land-use gradients. These results indicate that intensified management of ecosystems for resource extraction can increase their vulnerability to future disturbances.

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[1] This Chapter has been published as:
Laliberté, E., Wells, J. A., DeClerck, F., Metcalfe, D. J., Catterall, C. P., Queiroz, C., Aubin, I., Bonser, S. P., Ding, Y., Fraterrigo, J. M., McNamara, S., Morgan, J. W., Sánchez-Merlos, D., Vesk, P. A. and Mayfield, M. M. (2010). Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology Letters* 13:76–86.

6.2 Introduction

The unprecedented rates and global extent of current biodiversity loss (Pimm et al., 1995) have prompted a rapidly growing body of research exploring its functional consequences (Chapin et al., 2000; Loreau et al., 2001; Hooper et al., 2005). Although experimental studies have shown positive relationships between biodiversity and the rates or stability of various ecosystem functions (Balvanera et al., 2006), many of these studies have been criticised as marginally relevant to policy and management because they used random synthetic assemblages of species without considering the actual drivers of biodiversity loss (Srivastava and Vellend, 2005; Larsen et al., 2005; Leps, 2004). Moreover, most of these studies have presented species richness as their only measure of biodiversity (Balvanera et al., 2006) and did not assess functional diversity as a more direct and mechanistic link to ecosystem processes (Díaz and Cabido, 2001; Hooper et al., 2005).

In particular, a key aspect of functional diversity that has generated much interest is the variability of responses to environmental change among species that contribute similarly to ecosystem function (Chapin et al., 1997; Yachi and Loreau, 1999; Norberg et al., 2001; Naeem and Wright, 2003). This important yet largely unexplored facet of functional diversity has been termed "response diversity", and is considered crucial for ecosystem renewal and reorganization following disturbances (Chapin et al., 1997; Elmqvist et al., 2003). Response diversity represents the first safeguard against the loss of ecosystem functions and services in a changing world (Elmqvist et al., 2003; Folke et al., 2004). For example, in Californian serpentine grasslands, long-term studies over > 20 years showed that diverse responses of component species to rainfall variation and prolonged drought resulted in greater stability of primary production in the face of changing external conditions (Hobbs et al., 2007).

Response diversity has developed from the earlier concept of functional redundancy (Walker, 1992; Lawton and Brown, 1993; Naeem, 1998). If there are sets of co-existing species whose ecological effects are similar, then any given species pool may be classified into "functional effect groups", based on the traits which determine these effects (Hooper et al., 2002; Lavorel and

Garnier, 2002). The degree of redundancy within a functional effect group is the number of species it contains (Walker, 1992; Naeem, 1998). High redundancy provides resilience (sometimes called "insurance") against the loss of functions and services provided by that group if different species show compensatory responses following environmental change (Naeem, 1998). This view, however, is only valid if species richness corresponds directly to response diversity. This relationship cannot be assumed. If, for example, a large number of species within an effect group respond similarly to disturbance or environmental change, then functional redundancy would appear to be high even though response diversity is low (Elmqvist et al., 2003).

Despite calls to quantify how human-driven changes in biodiversity alter the ability of ecosystems to cope with future environmental change (e.g., Chapin et al., 1997; Scheffer et al., 2001; Folke et al., 2004; Foley et al., 2005), conceptual and theoretical development still greatly outpaces empirical application. So far, some field studies have demonstrated the existence of response diversity in plant or animal communities by observing responses to an anthropogenic disturbance event, but none has yet asked how response diversity itself can be altered by human activities. For example, Walker et al. (1999) found evidence for response diversity in an Australian rangeland by observing that minor plant species took over the functional roles of the dominant species following long-term grazing. Similarly, native bee communities in watermelon fields were shown to harbour elements of differing responses following the partial clearance of adjacent native vegetation cover, stabilizing pollination services to crops (Winfree and Kremen, 2009). While both studies have illustrated response diversity, neither have attempted to quantify how it can be impacted.

Globally, changing land-use patterns is the most important driver of biodiversity loss (Sala et al., 2000). Land-use change involves two main impacts on the biosphere: conversion (i.e., natural habitats altered for human use) and intensification (e.g., greater intensity and/or frequency of disturbance, increased use of external inputs; Foley et al., 2005). While the global impact of land-use change on species loss can be quantified (Pimm and Raven, 2000), its impacts on functional diversity and the long-term provisioning of ecosystem services remain much less clear. Recent studies have demon-

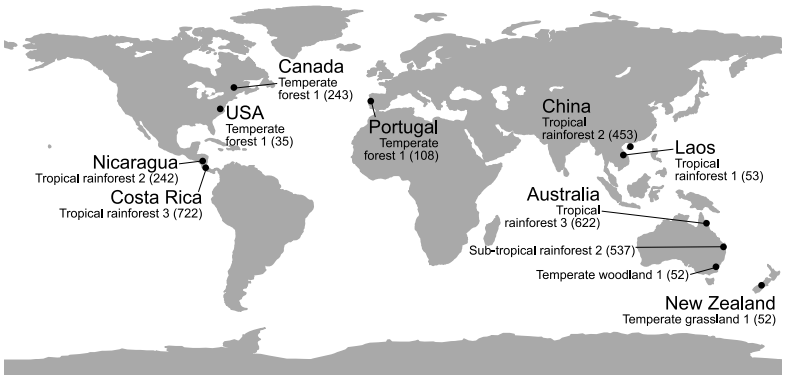

Figure 6.1: Map of study regions contributing to the meta-analysis. The map shows the major biome of each region, the number of distinct land-use intensity gradients, and total number of species (in parentheses).

strated changes in functional diversity of plant or animal assemblages in human-modified landscapes (e.g., Mayfield et al., 2006; Flynn et al., 2009), but none has yet examined how land-use change affects response diversity in particular.

This study explores how land-use change impacts plant functional redundancy and response diversity through a meta-analysis of 18 land-use intensity gradients from five biomes and nine countries, comprising more than 2800 species (Fig. 6.1). The intensification gradients include forest conversion to pasture, rangeland development, and logging regimes differing in intensity or frequency. A hierarchical effect-response functional trait framework (Hooper et al., 2002) is followed to measure response diversity based on the distinction between effect traits and response traits (Naeem and Wright, 2003; Hooper et al., 2002; Lavorel and Garnier, 2002; Suding et al., 2008). Species are first classified within each land-use intensity gradient into functional effect groups, using 12 traits that affect biogeochemical processes. The response diversity of each effect group is then quantified as the dispersion of its constituent species in response trait space, using 12 traits that affect plant responses to disturbances. The results show that land-use intensification generally leads to reductions in both response diversity and functional redundancy, thereby reducing ecosystem resilience to future disturbances.

Study	Biome	Land-use intensity gradient	Reference(s)
Australia / Tully	TR	Forest disturbance, clearance	Unpublished data
Australia / Mungalli	TR	Forest conversion to pasture	Unpublished data
Australia / Atherton	TR	Forest conversion to pasture/agriculture	(Kanowski et al., 2003)
Australia / QLD	STR	Forest conversion to pasture/agriculture	(Kanowski et al., 2003)
Australia / NSW	STR	Forest conversion to pasture/agriculture	(Kanowski et al., 2003)
China / Hainan lowland	TR	Logging or shifting agriculture	(Ding and Zang, 2009)
China / Hainan montane	TR	Logging or shifting agriculture	(Deng et al., 2008)
Laos	TR	Shifting agriculture	(Sheil et al., 2003)
Costa Rica / Las Cruces	TR	Forest conversion to pasture	(Mayfield et al., 2005, 2006)
Costa Rica / La Palma	TR	Forest conversion to pasture	(Mayfield et al., 2005, 2006)
Costa Rica / Puerto Jimenez	TR	Forest conversion to pasture	(Mayfield et al., 2005, 2006)
Nicaragua / Matiguas	TR	Forest conversion to pasture	(Sánchez et al., 2005b)
Nicaragua / Rivas	TR	Forest conversion to pasture	(Sánchez et al., 2005a)
New Zealand	TG	Fertilisation, irrigation, grazing intensity	(this thesis; Scott, 1999)
Australia / NSW	TW	Logging, thinning, grazing	(Thompson and Eldridge, 2005)
Portugal	TF	Forest conversion to pasture	Unpublished data
Canada / Québec	TF	Forest logging, conversion to pasture	(Aubin et al., 2007, 2009)
USA / North Carolina	TF	Forest logging, conversion to pasture	(Pearson et al., 1998)

Table 6.1: Summary of the 18 data sets included in this meta-analysis. STR = sub-tropical rainforest, TF = temperate forest, TG = temperate grassland, TR = tropical rainforest, TW = temperate woodland.

6.3 Materials and Methods

6.3.1 Study Regions

The data used in this study came from 18 land-use intensity gradients (Table 6.1), each from geographically distinct landscapes within 10 different regions around the globe (Fig. 6.1). These 18 studies covered five biomes (tropical rainforest, sub-tropical rainforest, temperate forest, temperate woodland, and temperate grassland) in a total of nine countries (Australia, Canada, China, Costa Rica, Laos, New Zealand, Nicaragua, Portugal, and the United States of America; Fig. 6.1). Datasets used in this study were made available to us by participants in an ARC-NZ vegetation function working group (http://www.vegfunction.net).

To identify appropriate data sets, coordinators of this working group approached ecologists who had published results on plant species and functional diversity from a human-altered landscapes. The aim was to identify appropriate data sets from diverse regions of the world, but not more than three data sets for any one global region. Of the data sets initially made available for this project, 18 studies proved appropriate for analysis. Datasets were used for the analyses if they included a survey of plant communities within a well-defined local geographic region, across plots representing a gradient of at least three land-use intensities relevant to that landscape, e.g., from

primary rainforest to logged sites or shifting cultivation fallows, or from ungrazed sub-alpine grasslands to heavily fertilised and grazed sites, and had equal sampling at each study site.

Land-use intensity was ranked on an ordinal scale specific to each landscape according to the intensity and/or frequency of disturbance (i.e., biomass removal) and external inputs (e.g., fertiliser). Vegetation was surveyed in one to 24 plots per land-use intensity, depending on the study. Within each study, standardised sampling methods were used to ensure consistent sampling of all plots. The vegetation surveys included all vascular terrestrial species, except in six studies which focused on particular life-forms (e.g., herbaceous or trees/shrubs) or plants within given size limits (e.g., all plants $>$ 1 cm diameter at breast height).

6.3.2 Plant Functional Traits

A common set of standardised functional traits (Table 6.2) was compiled to allow meaningful comparisons between the 18 data sets used in this study. In many cases, trait data were transformed and/or reclassified using traits gathered for the original studies. When this was not possible, new trait data were obtained from published sources or from herbarium specimens. Each individual study had between seven and 16 out of a possible 22 traits. Across all data sets, the functional trait analysis included 2871 species from 1290 genera and 255 families.

A crucial step in the methodological approach was to distinguish between effect and response traits (Table 6.2). This distinction is fundamental to the concept of response diversity (Hooper et al., 2002; Naeem and Wright, 2003). Effect traits were defined as traits that influence biogeochemical processes, while response traits were primarily regenerative traits that influence how species respond to disturbances (Lavorel and Garnier, 2002). Distinguishing between effect and response traits can be challenging (Suding et al., 2008). To guide this assessment, the recommendations of Cornelissen et al. (2003) for which traits fall into these categories were followed. Twelve effect and 12 response traits were designated, two of which were classified as relevant to both categories (Table 6.2).

Functional trait	E/R	Type	Units	Number of studies
Growth form	E	Nominal	-	17
Height	E	Continuous	m	15
Leaf dry matter content (LDMC)	E	Continuous	mg g^{-1}	2
Leaf nitrogen concentration (LNC)	E	Continuous	mg g^{-1}	1
Leaf phenology	E	Nominal	-	11
Leaf phosphorous concentration (LPC)	E	Continuous	mg g^{-1}	1
Leaf area	E	Continuous	mm^2	14
Leaf sulphur concentration (LSC)	E	Continuous	mg g^{-1}	1
Photosynthetic pathway	E/R	Nominal	-	8
Specific leaf area (SLA)	E	Continuous	m^2 kg^{-1}	10
Wood density	E/R	Continuous	kg m^{-3}	12
Nutrient uptake strategy	E/R	Nominal	-	13
Age of reproduction	R	Ordinal	-	1
Clonality	R	Nominal	-	10
Dispersal mode	R	Nominal	-	18
Lifespan	R	Ordinal	-	8
Maximum propagule longevity	R	Ordinal	-	7
Physical defence	R	Nominal	-	14
Pollination syndrome	R	Nominal	-	15
Raunkiaer life form	E/R	Nominal	-	7
Resprouting ability	R	Nominal	-	9
Seed mass	R	Continuous	mg	17

Table 6.2: Plant functional effect (E) and response (R) traits used in the analysis, and number of studies that included each trait.

6.3.3 Functional Redundancy and Response Diversity

The methodological approaches to measuring functional redundancy and response diversity are illustrated in Figures 6.2 and 6.3, respectively. For each data set, a Gower dissimilarity matrix was computed between all species (Figs. 6.2a and 6.3a), using effect traits (Table 6.2). This measure was chosen because it allows mixed variable types (continuous, ordinal, and categorical), as well as missing values (Legendre and Legendre, 1998; Podani, 1999). Effect traits were selected from the list in Table 6.2, excluding any traits that had very low coverage ($> 50\%$ missing values) or showed little or no variability; this was done on a per study basis.

Species were classified into functional effect groups using Ward's minimum variance clustering on the Gower dissimilarity matrix computed from effect traits (Figs. 6.2b and 6.3b). Ward's clustering method minimises within-group sums of squares and tends to form hyperspherical clusters with roughly the same number of species per cluster if species are evenly distributed in trait space (Legendre and Legendre, 1998). The actual number of effect groups for each data set was determined by visual inspection of the clustering dendrogram according to expert botanical knowledge, following Aubin et al. (2009).

Effect group membership was assigned to all species present in each plot (Figs. 6.2c and 6.3d), and the functional redundancy (number of species within an effect group; Fig. 6.2d) and response diversity of each effect group in each plot were estimated (Fig. 6.3c–e). Response diversity of each effect group was quantified by measuring the multivariate functional dispersion (see Chapter 2) of its constituent species in response trait space, based on a Gower dissimilarity matrix of species computed from response traits (Table 6.2). As with effect traits, the number and identity of response traits varied by data set.

Because FDis is the average distance of individual species to their group centroid in response trait space, it is little influenced by species number (see Chapter 2), contrary to other indices such as functional richness (FRic; Villéger et al., 2008) or functional attribute diversity (FAD; Walker et al., 1999) which are strongly positively influenced by the number of species. Therefore,

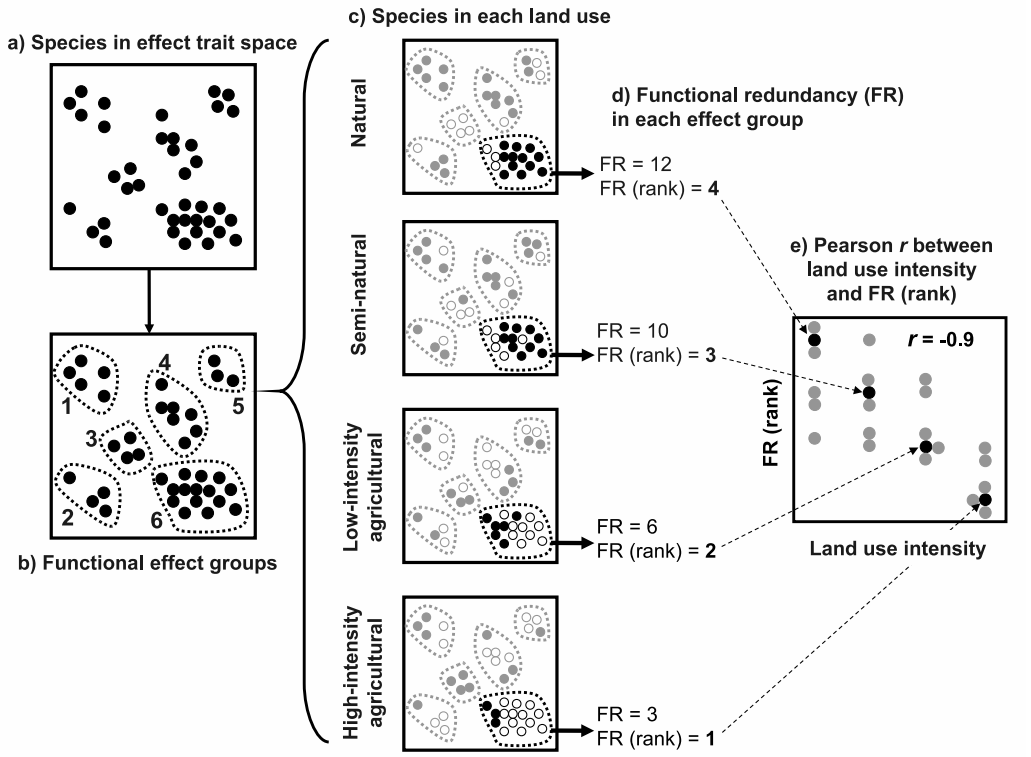

Figure 6.2: Overview of the methodological approach used to quantify changes in functional redundancy (FR) across a land-use intensity gradient. A species × species Gower dissimilarity matrix is computed from effect traits (**a**), from which species are classified into functional effect groups based on Ward's minimum variance clustering (**b**). For each sampling plot within each land use (**c**), FR is measured as the number of species within each group (**d**). Values are calculated for each effect group in each survey plot, and these values are ranked within effect groups to control for inter-group differences (**d**). For clarity, the example shows one effect group from one plot for each land-use intensity (the actual studies surveyed 1 to 24 plots per land-use intensity). Pearson correlation coefficients (r) are calculated between land-use intensity and ranked-within-group FR (**e**). The correlation coefficients from each study are then used as the effect sizes in the meta-analyses. For clarity, the diagram emphasises one particular functional effect group (in black) for steps **c**–**e**, although the same steps were performed for each of the other effect groups (in grey). The 24 data points in (**e**) represent six effect groups × four land-use types, and are jittered so that all can be viewed.

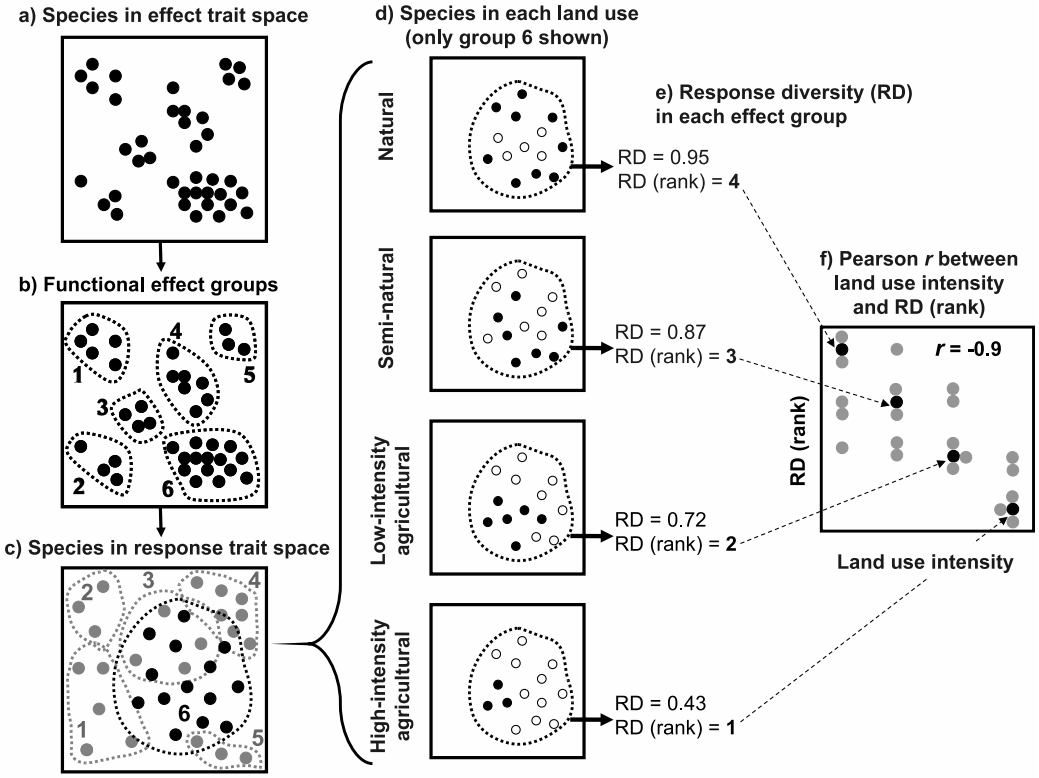

Figure 6.3: Overview of the methodological approach used to quantify changes in response diversity (RD) across a land-use intensity gradient. A species × species Gower dissimilarity matrix is computed from effect traits (**a**), from which species are classified into functional effect groups based on Ward's minimum variance clustering (**b**). Species can also be represented in response trait space, based on their response traits (**c**). For each sampling plot within each land use (**d**), RD is measured as the functional dispersion of these species in response trait space (**e**). Values are calculated for each effect group in each survey plot, and these values are ranked within effect groups to control for inter-group differences (**e**). For clarity, the example shows one effect group from one plot for each land-use intensity (the actual studies surveyed 1 to 24 plots per land-use intensity). Pearson correlation coefficients (r) are calculated between land-use intensity and ranked-within-group RD (**f**). The correlation coefficients from each study are then used as the effect sizes in the meta-analyses. For clarity, the diagram emphasises one particular functional effect group (in black) for steps **c**–**f**, although the same steps were performed for each of the other effect groups (in grey in c and e). The 24 data points in (**f**) represent six effect groups × four land-use types, and are jittered so that all can be viewed.

the use of FDis ensured that the response diversity measure was not trivially related to functional redundancy.

The index of response diversity was purposefully not weighted by species relative abundances because rare species may contribute substantially to resilience (Walker et al., 1999). A decrease in multivariate dispersion in response trait space (i.e., a loss of response diversity) for a given effect group means that its composition has shifted towards species that are more similar to each other in how they respond to disturbance, thereby indicating a loss of resilience. If, in a given plot, an effect group contained no species or only one species (in which case no multivariate dispersion can be computed), it was assigned a response diversity value of zero.

6.3.4 Meta-Analysis

For each of the 18 data sets (Table 6.1), all effect groups from all plots were used as individual observations. Therefore, the total number of observations is equal to the number of effect groups multiplied by the total number of plots, each plot representing an independent measurement. First, response diversity and functional redundancy were ranked between plots within each effect group to control for inter-group differences (e.g., as 1 to 10 if there were 10 plots; Figs. 6.2d and 6.3e). The Pearson correlation coefficient between land-use intensity (ordinal variable with different number of classes, depending on the data set) and either ranked within-group response diversity (Fig. 6.3f) or ranked within-group functional redundancy was then computed (Fig. 6.2e). This is conceptually equivalent to using the Spearman rank correlation, with the exception that ranking occurs within each group and not across all groups. Correlation coefficients were used as effect sizes in a formal meta-analysis across all data sets using the random-effect DerSimonian-Laird approach (Schulze, 2004). The aims with these meta-analyses were to: (i) estimate the mean effect of land-use intensification on response diversity and functional redundancy across all studies, and (ii) test the null hypotheses that land-use intensification has no effect on response diversity or functional redundancy.

In contrast to meta-analytical approaches based on fixed-effect models,

the DerSimonian-Laird approach is more conservative and shows an acceptable Type-I error rate when individual studies differ substantially (Schulze, 2004). Importantly, fixed-effect models limit inference to the sample in hand, while random-effect models allow more general inferences about a wider population. In the DerSimonian-Laird approach, correlations are first transformed using Fisher's z-transformation,

$$z_r = \frac{1}{2} \ln\left(\frac{1+r}{1-r}\right)$$

where r is the Pearson correlation coefficient. The asymptotic variance of z_r is calculated as $v_z = \frac{1}{(n-3)}$, where n is the sample size (number of effect groups $\times$ number of plots; Fig. 6.2e and 6.3f). Unlike r which is bounded between -1 and 1, z_r ranges from $-\infty$ to $+\infty$. Negative values of z_r indicate a negative association between response diversity (or functional redundancy) and land-use intensity. The mean effect size represents the average relationship between land-use intensity and the response diversity or functional redundancy of all effect groups from all 18 studies. 95% confidence intervals were computed as described by Schulze (2004). The `metacor` package (Laliberté, 2009) for R (R Development Core Team, 2010) was used to perform meta-analysis.

6.3.5 Null Models

To explore whether changes in response diversity could be distinguished from changes in functional redundancy, a null model approach was used. For each effect group in each community, a null distribution of 999 response diversity values was generated by randomly selecting species within the entire group while holding species number (i.e., functional redundancy) constant. Tests exploring whether the observed response diversity value for that effect group within each land use was lower than the null distribution at $\alpha = 0.05$ were performed. Groups containing zero or only one species, or groups containing all possible species from that group, were excluded since no meaningful null distributions could be generated in these cases. A larger occurrence of cases where response diversity is significantly ($P \leq 0.05$) lower than expected

from the null distribution following land-use intensification would suggest the creation of novel environmental filters limiting the breadth of species responses to disturbances within effect groups.

6.4 Results

The number of functional effect groups identified in each study ranged from two to 11, based on multivariate clustering analyses. Functional effect groups were generally distinguished by growth form, with further subdivisions provided by differences in nutrient uptake strategy, height, specific leaf area, or photosynthetic pathway. Land-use intensification was associated with an overall loss of functional redundancy in 13 out of 18 data sets, with z_r values ranging from -1.234 to 0.122 (Fig. 6.4a). Nine of the 13 negative z_r values, and only one of the five positive z_r values, were significantly ($P \leq 0.05$) different from zero (Fig. 6.4a). The mean effect size was -0.286 and differed significantly from zero ($P \leq 0.0001$; Fig. 6.4a), leading to the rejection of no change, and to the conclusion that functional redundancy declined at higher land-use intensities on average.

The relationship between land-use intensity and the response diversity of all effect groups within a given data set was negative in 9 out of 18 data sets and ranged from -0.430 to 0.201 (Fig. 6.4b), although only five of the negative and one of the positive z_r values were significantly ($P \leq 0.05$) different from zero (Fig. 6.4b). The mean effect size was -0.089, leading to rejection of the null hypothesis of no change in response diversity under land-use intensification ($P = 0.046$; Fig. 6.4b). This indicates that overall, and within several of the ecosystems studied, response diversity was reduced as land use intensified.

Although the FDis index used to measure response diversity is by construction little influenced by species richness (see Chapter 2), meta-analysis showed that response diversity and functional redundancy were positively associated in 14 out of 18 studies ($\bar{z}_r = 0.631$, $P \leq 0.0001$; Fig. 6.5). This was reflected in the similarity of results for functional redundancy (Fig. 6.4a) and response diversity (Fig. 6.4b). There was no evidence that response diversity was lower than expected from a null distribution as land use inten-

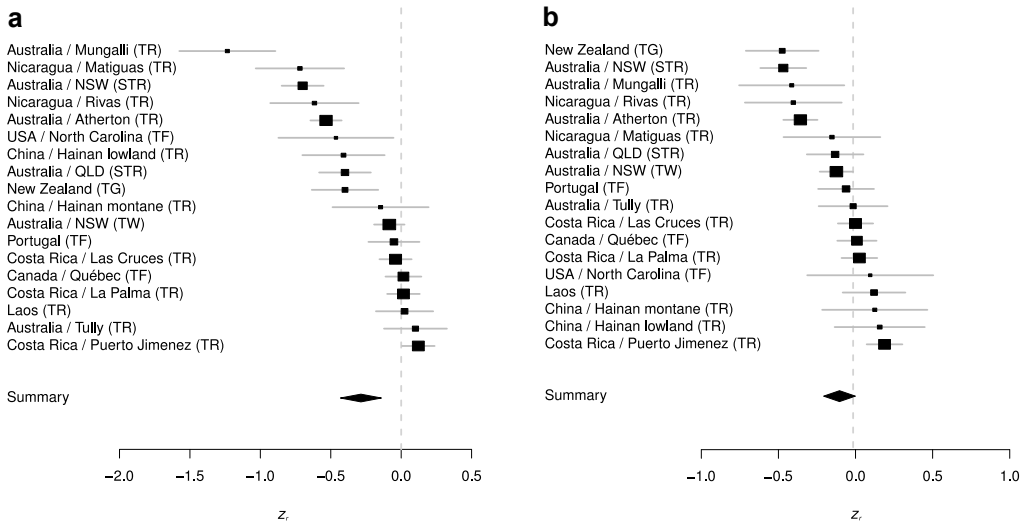

Figure 6.4: Meta-analyses of the effect of land-use intensification on (**a**) functional redundancy and (**b**) response diversity along 18 land-use intensity gradients. Effect sizes z_r are z-transformed Pearson correlation coefficients (r) between land-use intensity and ranked within-group functional redundancy or response diversity, following the DerSimonian-Laird approach. A negative value of z_r indicates a decrease in functional redundancy or response diversity as land use intensifies. Box size is proportional to the weight given to each study, based on sample size and variance. Grey lines are 95% confidence intervals (CI). The dashed grey line represents the null hypothesis. The summary statistic is represented by a black diamond whose width corresponds to its 95% CI. TR = tropical rainforest, STR = sub-tropical rainforest, TG = temperate grassland, TW = temperate woodland, TF = temperate forest.

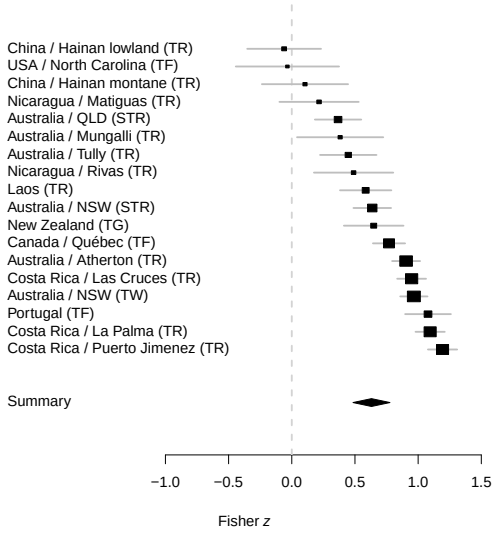

Figure 6.5: Meta-analysis of the association between response diversity and functional diversity across 18 land-use intensity gradients. Effect sizes z_r are z-transformed Pearson correlation coefficients between response diversity and functional redundancy, following the DerSimonian-Laird approach. See Figure 6.4 for details.

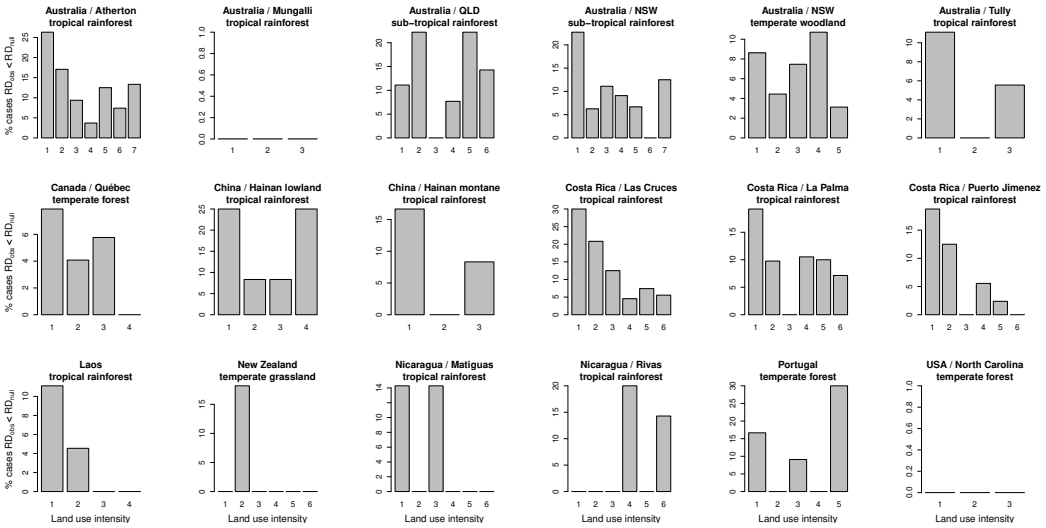

Figure 6.6: Percent of cases in each land-use intensity class where an effect group had a significantly ($P \leq 0.05$) lower response diversity than would be expected from a null distribution of values (representing random sampling of the same number of species as observed in each effect group in each land-use class).

sified (Fig. 6.6). On the contrary, in more than half of the studies (10 out of 18) response diversity was lower than expected most frequently in the least modified habitats (Fig. 6.6).

While meta-analysis pointed to general reductions in response diversity and functional redundancy under land-use intensification, patterns of individual effect groups included positive, negative, and more complex relationships (Figs. 6.7 and 6.8). Studies where land-use intensification led to relatively consistent reductions in the response diversity of individual effect groups (e.g., Australia / NSW sub-tropical rainforest and New Zealand grassland; Fig. 6.7) were the exception rather than the rule, as it was far more common for reductions in some groups to co-occur with minor or even large increases in others (Fig. 6.7). Similarly varied results were obtained for functional redundancy, though several studies showed more consistent reductions across groups (Fig. 6.7).

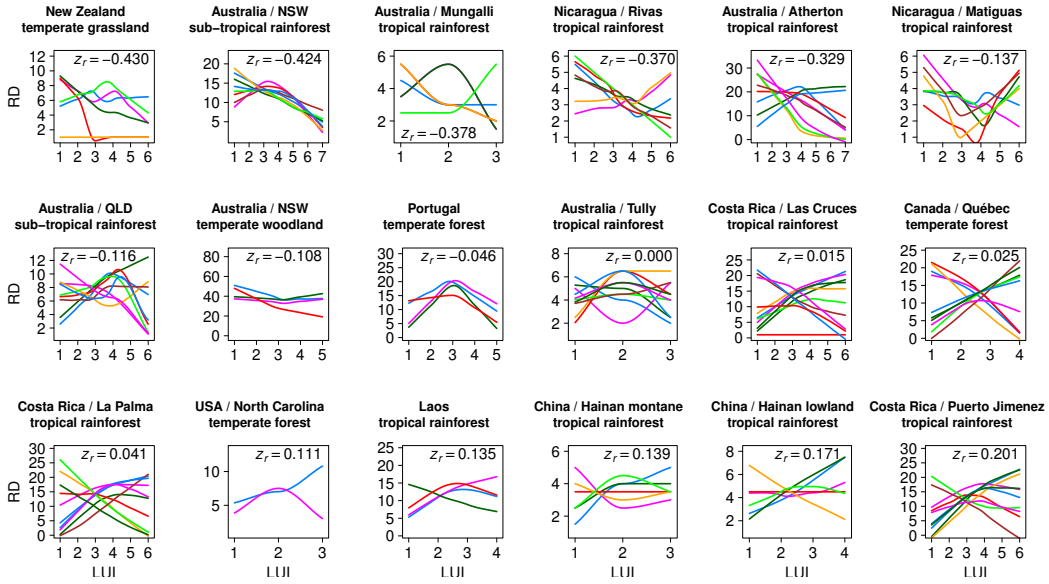

Figure 6.7: Response diversity (RD) of individual functional effect groups under increasing land-use intensity (LUI) for each of the 18 studies. For clarity, individual data points are omitted and only loess-smoothed curves are shown (span = 0.9). In each graph, curves of different colors represent different effect groups. RD is ranked within each effect group. z_r, the effect size used in the meta-analysis, is the z-transformed Pearson correlation coefficient (r) between RD and LUI computed from all effect groups. Graphs are laid out in increasing order of z_r, from left to right.

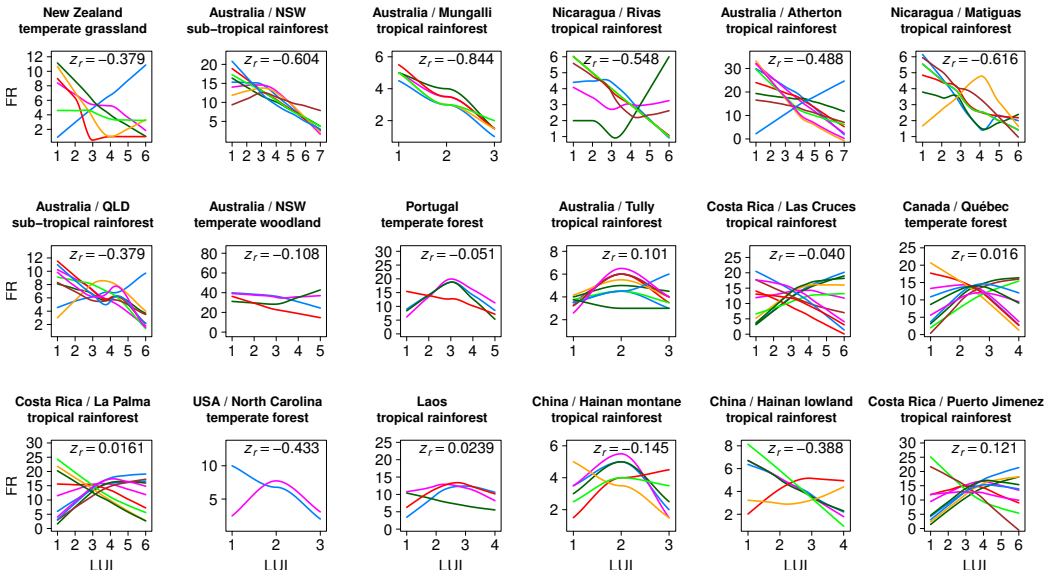

Figure 6.8: Functional redundancy (FR) of individual functional effect groups under increasing land-use intensity (LUI) for each of the 18 studies. See Figure 6.7 for details. To facilitate comparisons, graphs are laid out as in Figure 6.7.

6.5 Discussion

The meta-analysis shows that overall, and for the majority of studies considered, land-use intensification reduced functional redundancy and the diversity of responses to disturbance within groups of plants that have similar effects on biogeochemical processes (functional effect groups). Given the importance of functional redundancy and response diversity to ecosystem resilience (Walker, 1995; Elmqvist et al., 2003; Folke et al., 2004), this suggests that land-use intensification increases the vulnerability of functional effect groups to future disturbances. This occurs by reducing the number of species in each group (functional redundancy), and by reducing the response trait dispersion of each functional group (response diversity). These results support the view that maximising commodity supply (e.g., food, fuel, fibre, and timber) in the short term through intensified land management may jeopardise the long-term provisioning of ecosystem functions or services (Foley et al., 2005).

It is also important to recognise that ecosystems support multiple func-

tions simultaneously and require greater biodiversity than would be needed to sustain a single service (Hector and Bagchi, 2007). This capacity for provision of multiple services is best represented in the studies by the consideration of diverse traits, and their distributions in trait space. Because different functions are affected by variably distinct or overlapping sets of species, a focus on individual processes in isolation will underestimate levels of biodiversity required to maintain multifunctional ecosystems. As such, while this study does not address the resilience of any single service, its results do support the notion that the resilience of the suite of services offered by natural and semi-natural systems is compromised by land-use intensification.

The observed loss of functional redundancy is consistent with existing views of land-use intensification as one of the most important drivers of species loss worldwide, through its simplification of ecosystem structure (Sala et al., 2000; Pimm and Raven, 2000). For example, loss of functional redundancy in bird communities following land-use intensification in south-eastern Australia has been attributed to habitat simplification at the landscape scale (Fischer et al., 2008b). The more striking result to emerge from this study is the loss of response diversity under land-use intensification. The response diversity index (i.e., FDis; see Chapter 2) used in the present study in theory should be little influenced by functional redundancy. However, in practice the two measures were found to be positively associated. Moreover, response diversity was not lower than expected from a null distribution as land use intensified; in fact the opposite pattern was often observed. Taken together, these results invite the interpretation that sampling effects are the predominant cause of observed losses in response diversity under land-use intensification, where lower species richness decreases the probability of observing species with extreme trait values, tending to a narrower distribution. However, it is likely that the response traits are the objects of selection, and that species loss occurs because the traits are non-viable under changed conditions. It is not possible to distinguish these alternative interpretations with these analyses.

The results show that response diversity can increase or remain similar even concurrent with declines in functional redundancy, as seen for several individual effect groups, and also at the study-level in four data sets that

showed increases in response diversity with land-use intensification despite losses in functional redundancy (Fig. 6.4). Although such cases were rare, this suggests that response diversity can be maintained with lower levels of species richness if the remaining species are widely dispersed in response trait space.

Several studies showed no net impact of land-use intensification on response diversity or functional redundancy, and one even showed increases in both variables (Costa Rica / Puerto Jimenez). This may reflect, however, the focus of the Costa Rican studies on herb/shrub life-forms within a formerly forested landscape, where land-use intensification effectively corresponds to removal of trees and prevention of their re-establishment. This major, selective change in ecosystem structure may result from an alteration of environmental filters and enable establishment of herbaceous species with wider trait distributions than observed in closed forest (Mayfield et al., 2005, 2006). Extensive variation across effect groups and ecosystems suggests that the trajectories of change under land-use intensification depend jointly on the existing flora and disturbance regimes. Exploring which factors determined the response of individual effect groups to land-use intensification should be fertile ground for future empirical work, alongside questions on what parts of the response trait space are maintained or lost, and on the roles of spatial context and colonisation in the resilience of a focal ecosystem.

This study provides the first examination of how land-use change impacts response diversity. While it offers new insight, the effect-response framework used in this study presents some methodological challenges. First, it requires the assembly of a complete effect and response functional trait database for all (or most) species present in a community. This task may become easier as trait data sets covering large numbers of species are made accessible to the wider scientific community (e.g., Kleyer et al., 2008). Second, functional classifications should be based on traits that relate as directly as possible to an ecosystem function of interest (Naeem and Wright, 2003), yet we rarely know *a priori* exactly which traits are the most important (Petchey and Gaston, 2006). Further, we need to be sure that the response traits actually reflect differential responses to disturbances. Finally, classifying species into functional effect groups assumes some level of functional redundancy (Naeem and

Wright, 2003), but this should not always be taken for granted (Micheli and Halpern, 2005; Petchey et al., 2007), even in high-diversity systems (Bellwood et al., 2003). Indeed, redundancy is specific to particular functions and depends on the traits selected and methods for classification (Rosenfeld, 2002). Identifying effect groups involves an element of subjectivity, though decisions are based on the best-available ecological knowledge of the species considered (Aubin et al., 2009).

In this study species were classified based on their effect on biogeochemical processes such as primary productivity, litter decomposition, and nutrient cycling. The reason for this is two-fold. First, many ecosystem services directly depend on biogeochemical processes (Quétier et al., 2007b; Díaz et al., 2007a). Second, focusing on the traits that influence biogeochemical processes, on which some scientific consensus has emerged (Cornelissen et al., 2003), yielded a common currency for exploring changes in response diversity and functional redundancy under land-use intensification across a wide range of different ecosystems and biomes. An emerging frontier for further research will be a more targeted application of this methodological framework to groups of species that perform specific provisioning (e.g., forage production), cultural (e.g., native biodiversity), or regulating (e.g., flood interception) ecosystem services (Luck et al., 2009). Although recent progress has been made in identifying the links between plant traits and specific ecosystem services (Quétier et al., 2007a), this remains an important challenge for improving our understanding of how humans impact natural ecosystems (Díaz et al., 2007a).

6.6 Conclusions

There is an urgent need for ecologists to measure and predict how human activities erode response diversity and ecosystem resilience (Scheffer et al., 2001; Elmqvist et al., 2003; Folke et al., 2004) in order to detect early signs of ecological change before abrupt shifts occur (Scheffer et al., 2001). Through meta-analysis of 18 land-use intensity gradients from five biomes and nine countries, this study showed that land-use intensification was generally associated with a reduction in functional redundancy and response diversity

within groups of species that make similar contributions to ecosystem processes. Therefore, land-use intensification may decrease the resilience of ecosystems to future disturbances. Despite this general finding, responses of individual effect groups to land-use intensification within and across studies varied widely. Understanding the drivers of these patterns is a key direction for future research, especially to assess trade-offs or inter-dependence among ecosystem services under land-use change (DeFries et al., 2004; Foley et al., 2005). Quantifying response diversity within groups of species that perform particular services is a promising approach for assessing how vulnerable these services will be in an uncertain future, but more work is needed to develop our understanding of how environmental filters are involved in land-use change and the consequences losses of response diversity through human pressures.

Chapter VII

Conclusions

The main underlying theme of this thesis was that approaches based on functional traits (*sensu* Violle et al., 2007) may help us to better understand and predict changes in biodiversity in response to land-use change (Gross et al., 2007; Quétier et al., 2007b), as well as its potential feedbacks to ecosystem functions and services (Lavorel and Garnier, 2002; Díaz et al., 2007a; Suding et al., 2008) and ecosystem resilience to future environmental change (Elmqvist et al., 2003; Folke et al., 2004). The focus was on grazing systems, which are expected to undergo rapid intensification in fertiliser use and grazing pressure in the coming decades (Bouwman et al., 2005) to meet the growing global demand for livestock products (FAO, 2005). In particular, much of the work presented in this thesis focused on a long-term (27-year) experiment in which soil resource availability and grazing intensity were manipulated (Scott, 1999, see also Chapter 3).

This thesis was organised into five main chapters. First, a flexible framework for measuring different facets of functional diversity was described, and a new multidimensional functional diversity index, called functional dispersion (FDis), was also presented. Second, two vegetation sampling methods were compared with regard to their ability to detect changes in vegetation composition. Third, shifts in plant trait distributions following land-use changes were quantified and compared to null models, and a maximum entropy approach was used to quantify the direction and strength of selection on each trait. Fourth, it was shown that these shifts in trait distributions have cascading effects on primary production, litter decomposition, soil respiration, and ultimately, soil carbon sequestration. Finally, data from 18 land-use intensity gradients were used to show that land-use intensification reduces functional redundancy and response diversity, two components of

biodiversity that are thought to influence ecosystem resilience to future disturbances.

In this concluding chapter, the main findings from each chapter are summarised. Some future directions for trait-based research are then highlighted. Finally, general conclusions from the thesis, as well as some implications for management, are presented.

7.1 Summary

7.1.1 Measuring Functional Diversity

In Chapter 2, a highly flexible distance-based framework for measuring functional diversity from multiple traits was proposed. It allows one to measure different facets of functional diversity in multidimensional trait space from any distance or dissimilarity measure, any number of traits, and from different trait types (i.e., quantitative, semi-quantitative and qualitative), while also allowing for missing trait values and the weighting of individual traits. The need for abundance-weighted functional diversity metrics that describe the multivariate dispersion of species in multivariate trait space was emphasised, and a new multidimensional functional diversity index, called functional dispersion (FDis), was presented; this index is closely related to Rao's quadratic entropy (Rao, 1982; Botta-Dukát, 2005). FDis is the multivariate analogue of the weighted mean absolute deviation, in which the weights are species relative abundances. On the other hand, Rao's quadratic entropy is the multivariate analogue of the weighted variance. Therefore, FDis will be less affected than Rao's quadratic entropy by species with extreme trait values. In addition, for unweighted presence-absence data, FDis can be used for a formal statistical test of differences in functional diversity using distance-based tests of homogeneity of multivariate dispersions (Anderson, 2006). The `FD` R-language package was provided to easily implement this distance-based functional diversity framework.

7.1.2 Comparisons of Vegetation Sampling Methods

In Chapter 3, two sampling methods were compared in their ability to detect changes in vegetation composition following rangeland development: (i) species percent cover estimates within subplots (the percent cover method), and (ii) rankings of relative biomass of the ten most abundant species across the whole plot and the ratio of two of them (the visual ranking method). The results showed that the effect of vegetation sampling method was consistent across experimental treatments, indicating that both methods were equally good at detecting differences in vegetation composition following increases in fertiliser use and grazing pressure in grasslands. Effects of fertiliser on vegetation composition were an order-of-magnitude greater than the effect of sampling method, while the latter was twice as important as the effect of grazing. This reinforces previous findings that soil resource availability has a much greater impact on vegetation composition than grazing intensity in these grasslands (Scott, 2001, 2007). Overall, the results from Chapter 3 supported the use of the visual ranking method as a rapid yet powerful method for monitoring changes in vegetation composition under rangeland development in grasslands.

7.1.3 Plant Trait Responses

In Chapter 4, trait-based plant community assembly following long-term shifts in soil resource availability and grazing intensity was explored. Shifts in trait distributions were measured and compared to null models, and a maximum entropy approach was used to quantify the direction and strength of selection on each trait. Some insights into some of the key questions in trait-based research were obtained. First, the results provided further support for the importance of the nutrient acquisition–conservation trade-off as a primary axis of functional variation among plant species (Grime et al., 1997; Díaz et al., 2004; Wright et al., 2004), and for the presence of differences between native and exotic species along that axis (Leishman et al., 2007), with native species showing a distinct "stress-tolerant" strategy (*sensu* Grime, 2002). This last finding probably explains the marked loss of native plant species with fertilisation in these grasslands (Norton et al., 2006, see

also Chapter 4), likely due to competitive exclusion from fast-growing exotic species. This may reflect the particular evolutionary history of New Zealand grasslands, which prior to human occupation were not maintained by large mammalian herbivores or fire but were instead confined to marginal low-productivity sites (McGlone, 2001). On the other hand, previous studies found that native tussock species can benefit from fertiliser input, at least in terms of height growth (Scott, 2000a; Norton et al., 2006). While there was no qualitative evidence for such a pattern from the long-term experiment used in this thesis, this possibility deserves further attention, particularly because native tussocks are iconic elements in these landscapes.

Second, the results provided long-term experimental support for the hypothesis that slow-growing species become dominant under nutrient-poor environments because they hold a long-term advantage through leaf attributes that reduce nutrient losses (Chapin, 1980; Ryser, 1996; Aerts and Chapin, 2000; Grime, 2002). Third, the relative abundances of plant species from a common initial species pool were strongly influenced by functional traits across all experimental treatments, highlighting the importance of traits in determining relative abundance (Shipley et al., 2006b; Shipley, 2010b; Cornwell and Ackerly, 2010). Fourth, the direction and strength of selection on particular traits shifted with soil resource availability and sheep grazing intensity (Sonnier et al., 2010a), showing how different trait-based filters act under different environmental conditions. Finally, high soil resource availability led to strong trait under-dispersion due to competitive exclusion, whereas low soil resource availability led to trait over-dispersion due to limiting similarity. This challenges previous interpretations that trait under-dispersion should be more prevalent under increasing environmental stress, whereas limiting similarity should be more important in productive environments, where competition intensity is greatest (Weiher and Keddy, 1995; Weiher et al., 1998).

7.1.4 Feedbacks to Ecosystem Functioning

In Chapter 5, the response-effect trait framework (Lavorel and Garnier, 2002; Suding et al., 2008; Díaz et al., 2007a) was used to show that long-term ma-

nipulations of soil resource availability and grazing intensity in grasslands cause shifts in plant functional composition and diversity, with cascading effects on primary production, litter decomposition, soil respiration, and ultimately, soil carbon sequestration. The results showed that land-use intensification has cascading effects on ecosystem functioning, both through direct effects of changes to resource availability (Burke et al., 1997; Lambers et al., 2008a) and grazing (McNaughton et al., 1997), and through the indirect effects of these environmental forces on plant traits (Grime, 1998; Chapin et al., 2000; Quétier et al., 2007b) and functional diversity (Díaz and Cabido, 2001; Naeem and Wright, 2003; Heemsbergen et al., 2004). Not only did soil resource availability have the strongest effect on functioning, but it also moderated the effect of most other drivers. Indeed, this study provided strong experimental evidence that the effects of both functional diversity and herbivores on ecosystem functioning depend on soil resource availability (Fridley, 2002; Bardgett and Wardle, 2003) as they shifted from negative to positive with increasing soil resources. In particular, the results from this study suggest that increasing grazing pressure in marginal grasslands can lead to negative feedbacks on ecosystem functioning, potentially compromising long-term production potential. On the other hand, large concomitant increases in agricultural inputs and grazing intensity can lead to positive feedbacks on functioning, yet restrict opportunities for soil carbon sequestration. Chapter 5 illustrated how the use of plant traits and functional diversity can help us to better understand the functional consequences of changes in biodiversity from land-use intensification (Chapin et al., 2000; Hooper et al., 2005), thus helping to bridge the gap between community and ecosystem ecology (McGill et al., 2006).

7.1.5 Biodiversity and Ecosystem Resilience

Chapter 6 explored how land-use intensification impacts functional redundancy and response diversity in plant communities, using data from 18 land-use intensity gradients that represent five biomes and > 2800 species. Meta-analysis across all data sets showed that land-use intensification significantly reduced both functional redundancy and response diversity, although spe-

cific relationships varied considerably among the different land-use gradients. These results suggest that intensified management of ecosystems for resource extraction may increase the vulnerability to future disturbances of most functional groups of plant species. Despite the potential significance of this general finding, it is clear from Chapter 6 that more work is needed to develop our understanding of how environmental filters are involved in land-use change, and the consequences losses of response diversity through human pressures.

7.2 Future Directions

7.2.1 Intraspecific Functional Diversity

Measuring intraspecific variability for many functional traits, on many species can sometimes be too time-consuming or costly to be logistically feasible. As a way around this problem, most previous trait-based research, including many of the analyses presented in this thesis, have relied on the assumption that interspecific variability is much greater than intraspecific variability, focusing on mean trait values per species. However, recent work shows that intraspecific variability can be substantial (Albert et al., 2010), and this variability may be ecologically important. For example, Clark (2010) showed that individual (i.e., within-species) variation contributes to species coexistence in temperate forests; such individual variation may be partly due to intraspecific functional variability. Intraspecific variability can also influence ecosystem processes, for example litter decomposition rate (Lecerf and Chauvet, 2008). In addition, intraspecific variability may promote complementary resource use, similarly to resource complementarity among species. Therefore, a stronger consideration of intraspecific functional variability may be warranted in future trait-based research (Albert et al., 2010).

7.2.2 Modelling Trait Distributions

The data used in many trait-based community ecology research projects typically consist of (i) species $\times$ trait matrices, and (ii) a site $\times$ species abundances matrices. From these data, expected trait values (i.e., community-

weighted trait means) and/or various functional diversity metrics are generally computed, and then analysed. For example, these variables can be modelled separately, as done in Chapters 4 and 5. McGill et al. (2006) have strongly argued that further progress in community ecology will come through the use of trait-based approaches. However, Webb et al. (2010) recently stated that "traits-based studies arguably give the cumulative impression of an *ad hoc* collection of system-specific examples, rather than a body of literature organized around unifying principles". Webb et al. (2010) suggest that a way to unify approaches will be through modelling trait distributions directly, and using appropriate quantitative methods to test trait-based hypotheses. Traits would be measured at the individual level, such that trait distributions would include both intraspecific and interspecific variation, and be univariate or multivariate.

The main advantage of this approach is that tying trait distributions to statistical distributions would give access to the powerful arsenal of tools available in the maximum-likehood or Bayesian statistical frameworks (e.g., likelihood-based model selection approaches). For quantitative traits, using multivariate continuous distributions such as the multivariate normal distribution would be interesting, because not only expected values (i.e., means) could be modelled, but also variances and covariances as well (Shipley, 2010b). Shifts in trait variances along environmental gradients may reflect changes in the nature of strength of biotic interactions (Gross et al., 2009), while shifts in covariances may indicate whether parallel selection for particular combinations of traits occurs under some environmental conditions but not others (e.g., maximum height and specific leaf area may strongly covary under high resource availability and low disturbance intensity, yet may vary independently under lower soil resource availability greater disturbance intensity). However, for such an approach to become more widely used, ecologists will need to adapt their field sampling methods and start sampling traits directly (Gaucherand and Lavorel, 2007), instead of the more widely-used approach of measuring species abundances and traits separately. The former approach can actually be more efficient, especially in species-rich systems (Gaucherand and Lavorel, 2007).

7.2.3 Belowground Traits

Belowground traits (e.g., specific root length, average rooting depth, presence of specialised root structures) have received far less attention than aboveground traits (e.g., specific leaf area) in trait-based community ecology research, yet belowground traits could be particularly important in determining species abundances, especially in nutrient-limited ecosystems (Lambers et al., 2008b). Moreover, species coexistence and positive effects of biodiversity on ecosystem functioning are often explained in terms of complementary resource use (Chesson, 2000; Silvertown, 2004; Hooper et al., 2005), but it is still unclear whether aboveground traits are adequate proxies for belowground strategies (De Deyn et al., 2008). For example, fast-growing, "exploitative" species can show a "conservative" belowground strategy, and vice-versa (Personeni and Loiseau, 2004). In addition, it is being increasingly recognised that resource partitioning between different inorganic and organic forms of nitrogen and phosphorous occurs in the field (McKane et al., 2002; Silvertown, 2004; Turner, 2008; Bever et al., 2010), often facilitated by mycorrhizal fungi, but such ecologically important species differences are unlikely to be captured by "soft" (*sensu* Hodgson et al., 1999) aboveground traits such as specific leaf area and leaf nutrient concentrations. Despite the inherent difficulties associated with measuring belowground traits across a wide range of species, a stronger focus on belowground traits is needed in future trait-based research, particularly those traits that show a direct link to nutrient acquisition.

7.2.4 Extensions to the Maximum Entropy Model

Exploring environment–trait relationships has a long history in ecology (Schimper, 1898). What is novel in the maximum entropy model to community assembly (Shipley et al., 2006b, see also Chapter 4) is that it provides a logical and mathematical tool (Jaynes, 2003) for predicting the most likely species relative abundances at a site, given only a set of expected community-weighted traits (Shipley et al., 2006b). Though the model is promising (McGill, 2006), several questions and challenges remain:

Making the model more general The full potential of the maximum entropy approach to model community assembly rests on our future ability to predict community-weighted traits along environmental gradients (Shipley et al., 2007, 2006b). Indeed, it will only be possible to generalise the model if community-weighted trait means and variances vary predictably along environmental gradients. Although some recent progress has been made towards this goal (Shipley et al., 2010), this still remains largely unexplored. Methodological frameworks aimed at predicting community-wide trait distributions (and thus the constraints required by the maximum entropy model) along environmental gradients (Webb et al., 2010) hold promise. In addition, it is still unclear whether similar environmental conditions actually lead to similar trait distributions, regardless of the taxonomic composition of the regional species pool. Exploring this yet untested hypothesis would be possible through carefully-planned mesocosm experiments (Shipley, 2010b).

Selecting ecologically meaningful traits Traits have to be first selected based on their ecological relevance for a given system. As previously mentioned, belowground traits have yet to receive the full attention they merit. Chemical traits involved in defence against herbivores could also be important (Funk and Throop, 2010) but have been neglected. Moreover, instead of using highly inter-correlated traits (which can complicate interpretation; Shipley, 2010b), future studies should first try to screen a larger set of traits and only use traits that express as many independent axes of functional variation as possible.

When are traits not enough? Community assembly is not purely determined by local trait-based selection processes, but also by regional processes (e.g., dispersal). The maximum entropy model can explicitly consider differences in propagule pressure that are simply due to differences in species abundances across the landscape (Shipley, 2010b). Under what conditions does it become important to include this demographic element to improve predictions of the model?

Interspecific vs intraspecific functional variation Obviously, functional variation is not only present among species, but also within species – if it were not, evolution through natural selection could not occur. All recent applications of the model, including the one presented in this thesis (Chapter 4), work under the assumption that interspecific variation is much greater than intraspecific variation (Shipley et al., 2006b). It is possible to extend the model by using genotypes instead of species (Shipley, 2010b), but this has yet to be explored in empirical studies.

Single vs multiple functional optima Using community-aggregated traits as constraints in the model assumes a single "functional optimum" in the trait distribution (expressed as the mean). But what if multiple functional optima of approximately equal fitness were possible (Marks and Lechowicz, 2006), resulting in multimodal trait distributions? This question requires further investigation, first to explore whether such situations occur (and if so, when), and second how to best take them into account in the model.

7.2.5 The Response-Effect Framework and Structural Equation Modelling

The response-effect trait framework (Lavorel and Garnier, 2002; Suding et al., 2008; Díaz et al., 2007a) implies a series of connected events: changing environmental conditions drive shifts in trait distributions (means, variances), which can in turn influence ecosystem functioning. Because structural equation modelling (SEM) is an attractive way to represent and statistically test such causal hypotheses (Grace, 2006), it is likely to become an increasingly popular quantitative method to understand and predict the functional consequences of changing biodiversity. Although the use of SEM in Chapter 5 was limited to single traits (one in each model), which was justified by the fact that the traits used acted both as response and effect traits, response and effect traits may not always be the same (Lavorel and Garnier, 2002). In that case, SEM could be easily extended to consider more than one trait (and how they relate to each other), similarly to what Shipley et al. (2006a) have done to explore the fundamental trade-offs that generate the leaf economics spectrum (Wright et al., 2004). Because of its flexibility and ability to test complex multivariate hypotheses, a wider use of SEM could greatly benefit

trait-based research, and contribute to bridging the historical gap between community and ecosystem ecology (McGill et al., 2006).

7.2.6 Response Diversity of Ecosystem Service Providers

Understanding how human activities influence the long-term provision of ecosystem services is an important research goal (DeFries et al., 2004; Foley et al., 2005; Tscharntke et al., 2005; Carpenter et al., 2006; Bennett and Balvanera, 2007). In Chapter 6, a methodological framework was presented to measure response diversity, a component of biodiversity that is expected to influence resilience to future disturbances (Elmqvist et al., 2003; Folke et al., 2004). However, the link between the functional effect groups formed and the provision of particular ecosystem services was not clear. Advances in this field will be made by first identifying groups of "service-provider" species (Luck et al., 2009), and then estimating response diversity within these groups. In any case, experimental work is needed to first evaluate the importance of response diversity to resilience, which has yet to be determined. However, similarly to some early biodiversity-ecosystem function experiments whose results have been attributed to "sampling effects" (whereby the effects were driven by traits of particular species; Huston, 1997), it may be that the presence of particular response traits is more important than diversity *per se*. This hypothesis, however, remains untested.

7.3 Final Conclusions

Much of ecology has developed with species as the fundamental units of study. However, it has often been suggested that approaches based on functional traits are required to transform ecology into a more general, predictive science (Keddy, 1990; McGill et al., 2006; Webb et al., 2010). The research presented in this thesis illustrated how trait-based approaches to ecology can help us to understand changes in plant biodiversity following land-use intensification, and how these changes in plant biodiversity translate into effects on ecosystem functioning and ecosystem resilience. In the grasslands studied here, increased production through fertilisation strongly conflicts with plant biodiversity conservation; this is because native species exhibit a conservative

nutrient acquisition and use strategy, making them less competitive under the increased soil resources associated with fertilisation than faster-growing exotic species.

Changes in plant biodiversity following increases in soil resource availability and grazing pressure, in turn, influence the rates of ecosystem processes (primary production, litter decomposition, and soil respiration), and ultimately, soil carbon sequestration. Intermediate levels of fertilisation promoted soil carbon sequestration, yet high levels of fertilisation and irrigation actually reduced the potential of soils to store carbon, despite greatly increasing plant production (and thus agricultural potential). This indicates that a potential win-win situation between two ecosystem services, agricultural production and soil carbon sequestration, is possible at intermediate levels of fertilisation. On the other hand, fertilisation and grazing together appear to be largely incompatible with native plant biodiversity conservation in these grasslands; however, because these conclusions are mostly based from a single experiment where a large number of exotic species (25 species) were initially over-sown, extrapolation to other sites must be done with caution. Finally, the research results presented in this thesis also show that land-use intensification reduces plant response diversity and functional redundancy; this has been suggested in theoretical studies as reducing ecosystem resilience to future disturbances, although this remains to be demonstrated experimentally.

Overall, the results from this thesis suggest that: (i) in the absence of fertiliser inputs and irrigation, extensive sheep grazing appears to have little impact on plant biodiversity in these grasslands, although increasing grazing pressure can have negative impacts on litter decomposition, primary production, and ultimately, soil carbon sequestration; (ii) intermediate levels of fertilisation (without irrigation) increase production values and promote soil carbon sequestration, but lead to marked losses in native biodiversity, (iii) intensive land management (high fertilisation and irrigation) strongly increases production potential, yet reduces soil carbon sequestration potential and leads to greater losses of native plant biodiversity; and (iv) land-use intensification reduces plant response diversity and functional redundancy, which may reduce ecosystem resilience to future disturbances. By using

functional traits to understand how land-use changes lead to long-term shifts in plant biodiversity, and associated feedbacks to ecosystem functioning and ecosystem resilience, the work presented in this thesis highlights the potential of trait-based approaches to understand and forecast the functional consequences of shifts in biodiversity following global environmental changes.

Bibliography

Aarssen, L. W. (1997). High productivity in grassland ecosystems: affected by species diversity or productive species? *Oikos*, 80:183–184.

Ackerly, D. (2004). Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecological Monographs*, 74(1):25–44.

Adair, E. C., Hobbie, S. E., and Hobbie, R. K. (2010). Single-pool exponential decomposition models: potential pitfalls in their use in ecological studies. *Ecology*, 91(4):1225–1236.

Adler, P. B., Milchunas, D. G., Lauenroth, W. K., Sala, O. E., and Burke, I. C. (2004). Functional traits of graminoids in semi-arid steppes: a test of grazing histories. *Journal of Applied Ecology*, 41(4):653–663.

Aerts, R. (1995). The advantages of being evergreen. *Trends in Ecology & Evolution*, 10(10):402–407.

Aerts, R. (1999). Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks. *Journal of Experimental Botany*, 50(330):29–37.

Aerts, R., Caluwe, H. D., and Beltman, B. (2003). Plant community mediated vs. nutritional controls on litter decomposition rates in grasslands. *Ecology*, 84(12):3198–3208.

Aerts, R. and Chapin, F. S. (2000). The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research*, 30:1–67.

Aiken, L. S. and West, S. G. (1991). *Multiple Regression: Testing and Interpreting Interactions*. Sage Publications, Newbury Park, USA.

Albert, C. H., Thuiller, W., Yoccoz, N. G., Soudant, A., Boucher, F., Saccone, P., and Lavorel, S. (2010). Intraspecific functional variability: extent, structure and sources of variation. *Journal of Ecology*, 98(3):604–613.

Alexandratos, N. (1999). World food and agriculture: Outlook for the medium and longer term. *Proceedings of the National Academy of Sciences (USA)*, 96(11):5908–5914.

Allan, H. H. (1982). *Flora of New Zealand, Vol. I: Indigenous Tracheophyta - Psilopsida, Lycopsida, Filicopsida, Gymnospermae, Dicotyledons*. Botany Division, Department of Scientific and Industrial Research, Wellington, New Zealand.

Anderson, M. J. (2006). Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*, 62:245–253.

Anderson, M. J., Ellingsen, K. E., and McArdle, B. H. (2006). Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, 9(6):683–693.

Anderson, M. J., Gorley, R. N., and Clarke, R. (2008). *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods*. PRIMER-E, Plymouth, UK.

Anderson, M. J. and Robinson, J. (2003). Generalised discriminant analysis based on distances. *Australian & New Zealand Journal of Statistics*, 45:301–318.

Anderson, M. J. and Willis, T. J. (2003). Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology*, 84(2):511–525.

Archer, S., Schimel, D. S., and Holland, E. A. (1995). Mechanisms of shrubland expansion: land use, climate or CO_2? *Climatic Change*, 29:91–99.

Asner, G. P., Elmore, A. J., Olander, L. P., Martin, R. E., and Harris, A. T. (2004). Grazing systems, ecosystem responses, and global change. *Annual Review of Environment and Resources*, 29:261–299.

Asner, G. P. and Martin, R. E. (2009). Airborne spectranomics: mapping canopy chemical and taxonomic diversity in tropical forests. *Frontiers in Ecology and the Environment*, 7(5):269–276.

Atkin, O. K. and Tjoelker, M. G. (2003). Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in Plant Science*, 8(7):343–351.

Aubin, I., Gachet, S., Messier, C., and Bouchard, A. (2007). How resilient are northern hardwood forests to human disturbance? An evaluation using a plant functional group approach. *Écoscience*, 14(2):259–271.

Aubin, I., Ouellette, M. H., Legendre, P., Messier, C., and Bouchard, A. (2009). Comparison of two plant functional approaches to evaluate natural restoration along an old-field deciduous forest chronosequence. *Journal of Vegetation Science*, 20:185–196.

Augustine, D. J., Frelich, L. E., and Jordan, P. A. (1998). Evidence for two alternate stable states in an ungulate grazing system. *Ecological Applications*, 8(4):1260–1269.

Augustine, D. J. and McNaughton, S. J. (2007). Interactive effects of ungulate herbivores, soil fertility, and variable rainfall on ecosystem processes in a semi-arid savanna. *Ecosystems*, 9(8):1242–1256.

Bagchi, S. and Ritchie, M. E. (2010). Introduced grazers can restrict potential soil carbon sequestration through impacts on plant community composition. *Ecology Letters*, 13(8):959–968.

Balmford, A., Green, R. E., and Scharlemann, J. P. W. (2005). Sparing land for nature: exploring the potential impact of changes in agricultural yield on the area needed for crop production. *Global Change Biology*, 11:1594–1605.

Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J., Nakashizuka, T., Raffaelli, D., and Schmid, B. (2006). Quantifying the evidence for biodiversity

effects on ecosystem functioning and services. *Ecology Letters*, 9(10):1146–1156.

Bardgett, R. D. and Wardle, D. A. (2003). Herbivore-mediated linkages between aboveground and belowground communities. *Ecology*, 84(9):2258–2268.

Bellwood, D. R., Hoey, A. S., and Choat, J. H. (2003). Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecology Letters*, 6(4):281–285.

Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F., and Nyström, M. (2003). Reserves, resilience and dynamic landscapes. *Ambio*, 32(6):389–396.

Bennett, E. M. and Balvanera, P. (2007). The future of production systems in a globalized world. *Frontiers in Ecology and the Environment*, 5(4):191–198.

Bever, J. D., Dickie, I. A., Facelli, E., Facelli, J. M., Klironomos, J., Moora, M., Rillig, M. C., Stock, W. D., Tibbett, M., and Zobel, M. (2010). Rooting theories of plant community ecology in microbial interactions. *Trends in Ecology & Evolution*, 25(8):468–478.

Bolker, B. M. (2010). *bbmle: Tools for general maximum likelihood estimation. R package version 0.9.5.1.* The Comprehensive Archive R Network (CRAN), Vienna, Austria.

Botta-Dukát, Z. (2005). Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, 16(5):533–540.

Bouwman, A. F., der Hoek, K. W. V., Eickhout, B., and Soenario, I. (2005). Exploring changes in world ruminant production systems. *Agricultural Systems*, 84(2):121–153.

Buckland, S. M. and Grime, J. P. (2000). The effects of trophic structure and soil fertility on the assembly of plant communities: a microcosm experiment. *Oikos*, 91(2):336–352.

Bullock, J. M., Franklin, J., Stevenson, M. J., Silvertown, J., Coulson, S. J., Gregory, S. J., and Tofts, R. (2001). A plant trait analysis of responses to grazing in a long-term experiment. *Journal of Applied Ecology*, 38(2):253–267.

Burke, I. C., Lauenroth, W. K., and Parton, W. J. (1997). Regional and temporal variation in net primary production and nitrogen mineralization in grasslands. *Ecology*, 78(5):1330–1340.

Cailliez, F. (1983). The analytical solution of the additive constant problem. *Psychometrika*, 48:305–310.

Cardinale, B. J., Nelson, K., and Palmer, M. A. (2000). Linking species diversity to the functioning of ecosystems: on the importance of environmental context. *Oikos*, 91(1):175–183.

Carpenter, S. R., DeFries, R., Dietz, T., Mooney, H. A., Polasky, S., Reid, W. V., and Scholes, R. J. (2006). Millennium ecosystem assessment: research needs. *Science*, 314(5797):257–258.

Carpenter, S. R. and Folke, C. (2006). Ecology for transformation. *Trends in Ecology & Evolution*, 21(6):309–315.

Carpenter, S. R., Walker, B., Anderies, J. M., and Abel, N. (2001). From metaphor to measurement: resilience of what to what? *Ecosystems*, 765-781.

Cavender-Bares, J., Kozak, K. H., Fine, P. V. A., and Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology. *Ecology Letters*, 12(7):693–715.

Chapin, F. S. (1980). The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*, 11(1):233–260.

Chapin, F. S., Matson, P. A., and Mooney, H. A. (2002). *Principles of Terrestrial Ecosystem Ecology*. Springer, New York, USA.

Chapin, F. S., Walker, B. H., Hobbs, R. J., Hooper, D. U., Lawton, J. H., Sala, O. E., and Tilman, D. (1997). Biotic control over the functioning of ecosystems. *Science*, 277:500–504.

Chapin, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., Mack, M. C., and Díaz, S. (2000). Consequences of changing biodiversity. *Nature*, 405:234–242.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31:343–366.

Cingolani, A. M., Posse, G., and Collantes, M. B. (2005). Plant functional traits, herbivore selectivity and response to sheep grazing in Patagonian steppe grasslands. *Journal of Applied Ecology*, 42(1):50–59.

Clark, E. A. (2001). Diversity and stability in humid temperate pastures. In Tow, P. G. and Lazenby, A., editors, *Competition and Succession in Pastures*, pages 103–118. CAB International Publishing, New York, USA.

Clark, J. (2009). Beyond neutral science. *Trends in Ecology & Evolution*, 24(1):8–15.

Clark, J. S. (2010). Individuals and the variation needed for high species diversity in forest trees. *Science*, 327(5969):1129–1132.

Clark, J. S., Dietze, M., Chakraborty, S., Agarwal, P. K., Ibanez, I., LaDeau, S., and Wolosin, M. (2007). Resolving the biodiversity paradox. *Ecology Letters*, 10(8):647–659.

Clarke, R. and Gorley, R. N. (2006). *PRIMER v6: User Manual/Tutorial*. PRIMER-E, Plymouth, UK.

Clements, F. E. (1916). *Plant Succession: an Analysis of the Development of Vegetation*. Carnegie Institution of Washington, Washington DC, USA.

Cockayne, L. (1920). An economic investigation of the montane tussock-grassland of New Zealand. IX. further details regarding the Earnscleugh (central Otago) palatability experiment. *New Zealand Journal of Agriculture*, 21:324–334.

Coley, P. D., Bryant, J. P., and Chapin, F. S. (1985). Resource availability and plant antiherbivore defense. *Science*, 230(4728):895–899.

Connor, E. F. and Simberloff, D. (1979). The assembly of species communities: chance or competition? *Ecology*, 60(6):1132–1140.

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D. E., Reich, P. B., ter Steege, H., Morgan, H. D., van der Heijden, M. G. A., Pausas, J. G., and Poorter, H. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, 51(4):335–380.

Cornwell, W. K. and Ackerly, D. D. (2009). Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, 79(1):109–126.

Cornwell, W. K. and Ackerly, D. D. (2010). A link between plant traits and abundance: evidence from coastal California woody plants. *Journal of Ecology*, 98(4):814–821.

Cornwell, W. K., Schwilk, D. W., and Ackerly, D. D. (2006). A trait-based test for habitat filtering: convex hull volume. *Ecology*, 87(6):1465–1471.

Covacevich, N. (1991). *Environmental Selection of Pasture Species at Lake Tekapo*. PhD thesis, Lincoln University, Lincoln, New Zealand.

Craine, J. M. and Lee, W. G. (2003). Covariation in leaf and root traits for native and non-native grasses along an altitudinal gradient in New Zealand. *Oecologia*, 134(4):471–478.

Cruz, P., Quadros, F. L. F. D., Theau, J. P., Frizzo, A., Jouany, C., Duru, M., and Carvalho, P. C. F. (2010). Leaf traits as functional descriptors of the intensity of continuous grazing in native grasslands in the south of Brazil. *Rangeland Ecology & Management*, 63(3):350–358.

Cunningham, S. A., Summerhayes, B., and Westoby, M. (1999). Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. *Ecological Monographs*, 69(4):569–588.

Daly, M. J., Hunter, R. M., N., G. G., and Hunt, L. (1996). A comparison of multi-species pasture with ryegrass-white clover pastures under dryland conditions. *Proceedings of the New Zealand Grassland Association*, 58:53–58.

De Deyn, G. B., Cornelissen, J. H. C., and Bardgett, R. D. (2008). Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters*, 11(5):516–531.

DeFries, R. S., Foley, J. A., and Asner, G. P. (2004). Land-use choices: balancing human needs and ecosystem function. *Frontiers in Ecology and the Environment*, 2(5):249–257.

Della Pietra, S., Della Pietra, V., and Lafferty, J. (1997). Inducing features of random fields. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, 19(4):380–393.

Deng, F., Zang, R., and Chen, B. (2008). Identification of functional group in an old-growth tropical montane rain forest on Hainan Island, China. *Forest Ecology & Management*, 255:1820–1830.

Diamond, J. M. (1975). Assembly of species communities. In Cody, M. L. and Diamond, J. M., editors, *Ecology and Evolution of Communities*, pages 342–444. Harvard University Press, Cambridge, USA.

Dijkstra, P. and Lambers, H. (1989). Analysis of specific leaf area and photosynthesis of two inbred lines of *Plantago major* differing in relative growth rate. *New Phytologist*, 113(3):283–290.

Ding, Y. and Zang, R. (2009). Effects of logging on the diversity of lianas in a lowland tropical rain forest in Hainan Island, South China. *Biotropica*, 41(5):618–624.

Dobson, A. P., Bradshaw, A. D., and Baker, A. J. M. (1997). Hopes for the future: restoration ecology and conservation biology. *Science*, 277:515–522.

Dorrough, J. and Scroggie, M. P. (2008). Plant responses to agricultural intensification. *Journal of Applied Ecology*, 45(4):1274–1283.

Douglas, J. A. and Risk, W. H. (1981). Soil fertility studies in North Otago. 1. the effect of phosphorus, sulphur, and molybdenum on clover growth on a range of soils. *New Zealand Journal of Experimental Agriculture*, 9:47–55.

Duffy, J. E. (2009). Why biodiversity is important to the functioning of real-world ecosystems. *Frontiers in Ecology and the Environment*, 7(8):437–444.

Díaz, S. and Cabido, M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, 16(11):646–655.

Díaz, S., Cabido, M., and Casanoves, F. (1998). Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science*, 9(1):113–122.

Díaz, S., Fargione, J., Chapin, F. S., and Tilman, D. (2006). Biodiversity loss threatens human well-being. *PLoS Biology*, 4(8):e277.

Díaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., Montserrat-Martí, G., Grime, J. P., Zarrinkamar, F., Asri, Y., Band, S. R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M. C., Shirvany, F. A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Diez, A., Shaw, S., Siavash, B., Villar-Salvador, P., and Zak, M. R. (2004). The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science*, 15:295–304.

Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., and Robson, T. M. (2007a). Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences (USA)*, 104(52):20684–20689.

Díaz, S., Lavorel, S., III, F. S. C., Tecco, P. A., Gurvich, D. E., and Grigulis, K. (2007b). Functional diversity – at the crossroads between ecosystem functioning and environmental filters. In Canadell, J. G., Pataki, D., and Pitelka, L., editors, *Terrestrial Ecosystems in a Changing world*, The IGBP Series, pages 81–91. Springer-Verlag, Berlin.

Díaz, S., Lavorel, S., McIntyre, S. U. E., Falczuk, V., Casanoves, F., Milchunas, D. G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W. E. I., Clark, H., and Campbell, B. D. (2007c). Plant trait responses to grazing – a global synthesis. *Global Change Biology*, 13:313–341.

Díaz, S., Symstad, A. J., Chapin, F. S., Wardle, D. A., and Huenneke, L. F. (2003). Functional diversity revealed by removal experiments. *Trends in Ecology & Evolution*, 18(3):140–146.

Edgar, E. and Connor, H. E. (2000). *Flora of New Zealand, Vol. V: Graminae*. Maanaki Whenua Press, Lincoln, New Zealand.

Edwards, L. J., Muller, K. E., Wolfinger, R. D., Qaqish, B. F., and Schabenberger, O. (2008). An R^2 statistic for fixed effects in the linear mixed model. *Statistics in Medicine*, 27(29):6137–6157.

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., and Norberg, J. (2003). Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, 1(9):488–494.

Elser, J. J., Dobberfuhl, D. R., MacKay, N. A., and Schampel, J. H. (1996). Organism size, life history, and N:P stoichiometry. *BioScience*, 46(9):674–684.

Emerson, B. C. and Gillespie, R. G. (2008). Phylogenetic analysis of community assembly and structure over space and time. *Trends in Ecology & Evolution*, 23(11):619–630.

Epps, K. Y., Comerford, N. B., Reeves, I. I. I. J. B., Cropper, J. W. P., and Araujo, Q. R. (2007). Chemical diversity - highlighting a species richness and ecosystem function disconnect. *Oikos*, 116(11):1831–1840.

Estabrook, G. F. and Rogers, D. J. (1966). A general method of taxonomic description for a computed similarity measure. *BioScience*, 16:789–793.

Ewers, R. M., Scharlemann, J. P. W., Balmford, A., and Green, R. E. (2009). Do increases in agricultural yield spare land for nature? *Global Change Biology*, 15(7):1716–1726.

Fargione, J., Hill, J., Tilman, D., Polasky, S., and Hawthorne, P. (2008). Land clearing and the biofuel carbon debt. *Science*, 319(5867):1235–1238.

Faria, J. C. and Demetrio, C. G. B. (2009). *Biplot of Multivariate Data Based on Principal Components Analysis. R package version 1.0.3.* UESC and ESALQ, Ilheus, Bahia, Brasial and Piracicaba, Sao Paulo, Brasil.

Findlay, S., Carreiro, M., Krischik, V., and Jones, C. G. (1996). Effects of damage to living plants on leaf litter quality. *Ecological Applications*, 6(1):269–275.

Fischer, J., Brosi, B., Daily, G. C., Ehrlich, P. R., Goldman, R., Goldstein, J., Lindenmayer, D. B., Manning, A. D., Mooney, H. A., Pejchar, L., Ranganathan, J., and Tallis, H. (2008a). Should agricultural policies encourage land sparing or wildlife-friendly farming? *Frontiers in Ecology and the Environment*, 6(7):380–385.

Fischer, J., Lindenmayer, D., Blomberg, S., Montague-Drake, R., Felton, A., and Stein, J. (2008b). Functional richness and relative resilience of bird communities in regions with different land-use intensities. *Ecosystems*, 10(6):964–974.

Fischer, J., Lindenmayer, D. B., and Manning, A. D. (2006). Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. *Frontiers in Ecology and the Environment*, 4(2):80–86.

Flynn, D. F. B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B. T., Lin, B., Simpson, N., Mayfield, M. M., and DeClerck, F. (2009). Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters*, 12(1):22–33.

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N., and Snyder, P. K. (2005). Global consequences of land use. *Science*, 309(5734):570–574.

Foley, J. A., Monfreda, C., Ramankutty, N., and Zaks, D. (2007). Our share of the planetary pie. *Proceedings of the National Academy of Sciences (USA)*, 104(31):12585–12586.

Folke, C. (2006). The economic perspective: conservation against development versus conservation for development. *Conservation Biology*, 20(3):686–688.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., and Holling, C. S. (2004). Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, & Systematics*, 35(1):557–581.

Folke, C., Holling, C. S., and Perrings, C. (1996). Biological diversity, ecosystems, and the human scale. *Ecological Applications*, 6(4):1018–1024.

Food and of the United Nations (FAO), A. O. (2005). *Livestock Policy Brief O2*. FAO, Rome, Italy.

Fortunel, C., Garnier, E., Joffre, R., Kazakou, E., Quested, H., Grigulis, K., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Freitas, H., Golodets, C., Jouany, C., Kigel, J., Kleyer, M., Lehsten, V., Leps, J., Meier, T., Pakeman, R., Papadimitriou, M., Papanastasis, V. P., Quétier, F., Robson, M., Sternberg, M., Theau, J., Thébault, A., and Zarovali, M. (2009). Leaf traits capture the effects of land use changes and climate on litter decomposability of grasslands across Europe. *Ecology*, 90(3):598–611.

Fraser, L. H. and Grime, J. P. (1999). Interacting effects of herbivory and fertility on a synthesized plant community. *Journal of Ecology*, 87(3):514–525.

Fridley, J. D. (2001). The influence of species diversity on ecosystem productivity: how, where, and why? *Oikos*, 93(3):514–526.

Fridley, J. D. (2002). Resource availability dominates and alters the relationship between species diversity and ecosystem productivity in experimental plant communities. *Oecologia*, 132(2):271–277.

Friedel, M. and Chewings, V. (1988). Comparison of crown cover estimates for woody vegetation in arid rangelands. *Australian Journal of Ecology*, 13(4):463–468.

Funk, J. and Throop, H. (2010). Enemy release and plant invasion: patterns of defensive traits and leaf damage in Hawaii. *Oecologia*, 162(4):815–823.

Garnier, É. (1992). Growth analysis of congeneric annual and perennial grass species. *Journal of Ecology*, 80(4):665–675.

Garnier, É., Cortez, J., Billès, G., Navas, M., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., and Toussaint, J. (2004). Plant functional markers capture ecosystem properties during secondary sucession. *Ecology*, 85(9):2630–2637.

Garnier, É. and Laurent, G. (1994). Leaf anatomy, specific mass and water content in congeneric annual and perennial grass species. *New Phytologist*, 128(4):725–736.

Garnier, É., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C., Freitas, H., Golodets, C., Grigulis, K., Jouany, C., Kazakou, E., Kigel, J., Kleyer, M., Lehsten, V., Leps, J., Meier, T., Pakeman, R., Papadimitrio, M., Papanastasis, V. P., Quested, H., Quétier, F., Robson, M., Roumet, C., Rusch, G., Skarpe, C., Sternberg, M., Theau, J., Thébault, A., Vile, D., and Zarovali, M. P. (2007). Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Annals of Botany*, 99(5):967–985.

Garnier, É., Salager, J., Laurent, G., and Sonié, L. (1999). Relationships between photosynthesis, nitrogen and leaf structure in 14 grass species and their dependence on the basis of expression. *New Phytologist*, 143(1):119–129.

Garnier, É., Shipley, B., Roumet, C., and Laurent, G. (2001). A standardized protocol for the determination of specific leaf area and leaf dry matter content. *Functional Ecology*, 15(5):688–695.

Gaucherand, S. and Lavorel, S. (2007). New method for rapid assessment

of the functional composition of herbaceous plant communities. *Austral Ecology*, 32(8):927–936.

Gaudet, C. L. and Keddy, P. A. (1988). A comparative approach to predicting competitive ability from plant traits. *Nature*, 334(6179):242–243.

Gehring, C. A. and Whitham, T. G. (1994). Interactions between aboveground herbivores and the mycorrhizal mutualists of plants. *Trends in Ecology & Evolution*, 9(7):251–255.

Gessner, M. O., Swan, C. M., Dang, C. K., McKie, B. G., Bardgett, R. D., Wall, D. H., and Hättenschwiler, S. (2010). Diversity meets decomposition. *Trends in Ecology & Evolution*, 25(6):372–380.

Gillson, L. and Hoffman, M. T. (2007). Rangeland ecology in a changing world. *Science*, 315(5808):53–54.

Gitay, H. and Noble, I. R. (1997). What are functional types and how should we seek them? In Smith, T. M., Shugart, H. H., and Woodward, F. I., editors, *Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change*, pages 3–19. Cambridge University Press, Cambridge, UK.

Gleason, H. A. (1926). The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club*, 53(1):7–26.

Godínez-Alvarez, H., Herrick, J., Mattocks, M., Toledo, D., and Zee, J. V. (2009). Comparison of three vegetation monitoring methods: Their relative utility for ecological assessment and monitoring. *Ecological Indicators*, 9(5):1001–1008.

Gordon, L. J., Steffen, W., Jonsson, B. F., Folke, C., Falkenmark, M., and Johannessen, A. (2005). Human modification of global water vapor flows from the land surface. *Proceedings of the National Academy of Sciences (USA)*, 102(21):7612–7617.

Gotelli, N. J. and Ellison, A. M. (2004). *A Primer of Ecological Statistics*. Sinauer Associates Inc., Sunderland, MA, USA.

Gower, J. C. (1971). A general coefficient of similarity and some of its properties. *Biometrics*, 27(4):857–871.

Gower, J. C. (1982). Euclidean distance geometry. *Mathematical Scientist*, 7:1–14.

Gower, J. C. and Legendre, P. (1986). Metric and euclidean properties of dissimilarity coefficients. *Journal of Classification*, 3:5–48.

Grace, J. B. (2006). *Structural Equation Modeling and Natural Systems*. Cambridge University Press, Cambridge, UK.

Grace, J. B., Anderson, T. M., Smith, M. D., Seabloom, E., Andelman, S. J., Meche, G., Weiher, E., Allain, L. K., Jutila, H., Sankaran, M., Knops, J., Ritchie, M., and Willig, M. R. (2007). Does species diversity limit productivity in natural grassland communities? *Ecology Letters*, 10(8):680–689.

Green, R. E., Cornell, S. J., Scharlemann, J. P. W., and Balmford, A. (2005). Farming and the fate of wild nature. *Science*, 307(5709):550–555.

Grime, J. P. (1973). Competitive exclusion in herbaceous vegetation. *Nature*, 242:344–347.

Grime, J. P. (1974). Vegetation classification by reference to strategies. *Nature*, 250:26–31.

Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*, 111(982):1169–1194.

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, 86:902–910.

Grime, J. P. (2002). *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. John Wiley & Sons, West Sussex, UK, 2nd edition.

Grime, J. P., Thompson, K., Hunt, R., Hodgson, J. G., Cornelissen, J. H. C., Rorison, I. H., Hendry, A. F., Ashenden, T. W., Askew, A. P., Band, S. R., Booth, R. E., Bossard, C. C., Campbell, B. D., Cooper, J. E. L., Davison, A. W., Gupta, P. L., Hall, W., Hand, D. W., Hannah, M. A., Hillier, S. H., Hodkinson, D. J., Jalili, A., Liu, Z., Mackey, J. M. L., Matthews, N., Mowforth, M. A., Neal, A. M., Reader, R. J., Reiling, K., Ross-Fraser, W., Spencer, R. E., Sutton, F., Tasker, P. C., Thorpe, P. C., and Whitehouse, J. (1997). Integrated screening validates primary axes of specialisation in plants. *Oikos*, 79(2):259–281.

Gross, N., Kunstler, G., Liancourt, P., de Bello, F., Suding, K. N., and Lavorel, S. (2009). Linking individual response to biotic interactions with community structure: a trait-based framework. *Functional Ecology*, 23(6):1167–1178.

Gross, N., Robson, T. M., Lavorel, S., Albert, C., Bagousse-Pinguet, Y. L., and Guillemin, R. (2008). Plant response traits mediate the effects of subalpine grasslands on soil moisture. *New Phytologist*, 180(3):652–662.

Gross, N., suding, K. N., and Lavorel, S. (2007). Leaf dry matter content and lateral spread predict response to land use change for six subalpine grassland species. *Journal of Vegetation Science*, 18:289–300.

Gunderson, L. H. (2000). Ecological resilience - in theory and application. *Annual Review of Ecology and Systematics*, 31(1):425–439.

Gunderson, L. H. and Pritchard, L. (2002). *Resilience and the Behavior of Large-Scale Systems*. Island Press, Washington, D. C.

Haberl, H., Erb, K. H., Krausmann, F., Gaube, V., Bondeau, A., Plutzar, C., Gingrich, S., Lucht, W., and Fischer-Kowalski, M. (2007). Quantifying and mapping the human appropriation of net primary production in Earth's

terrestrial ecosystems. *Proceedings of the National Academy of Sciences (USA)*, 104(31):12942–12947.

Haegeman, B. and Loreau, M. (2008). Limitations of entropy maximization in ecology. *Oikos*, 117(11):1700–1710.

Haegeman, B. and Loreau, M. (2009). Trivial and non-trivial applications of entropy maximization in ecology: a reply to Shipley. *Oikos*, 118(8):1270–1278.

Hamilton, E. W. and Frank, D. A. (2001). Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. *Ecology*, 82(9):2397–2402.

Hamilton, E. W., Frank, D. A., Hinchey, P. M., and Murray, T. R. (2008). Defoliation induces root exudation and triggers positive rhizospheric feedbacks in a temperate grassland. *Soil Biology and Biochemistry*, 40(11):2865–2873.

Hardy, O. J. (2008). Testing the spatial phylogenetic structure of local communities: statistical performances of different null models and test statistics on a locally neutral community. *Journal of Ecology*, 96(5):914–926.

Harpole, W. S. and Tilman, D. (2007). Grassland species loss resulting from reduced niche dimension. *Nature*, 446(7137):791–793.

Hartley, A. E. and Schlesinger, W. H. (2000). Environmental controls on nitric oxide emissions from northern chihuahuan desert soils. *Biogeochemistry*, 50:279–300.

Hawkesford, M. J. (2007). Sulfur and plant ecology: a central role of sulfate transporters in responses to sulfur availability. In Hawkesford, M. J. and Kok, L. J. D., editors, *Sulfur in Plants: an Ecological Perspective*. Springer, Dordrecht, Netherlands.

He, F. (2010). Maximum entropy, logistic regression, and species abundance. *Oikos*, 119(4):578–582.

Hector, A. and Bagchi, R. (2007). Biodiversity and ecosystem multifunctionality. *Nature*, 448(7150):188–190.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M. C., Diemer, M., Dimitrakopoulos, P. G., Finn, J. A., Freitas, H., Giller, P. S., Good, J., Harris, R., Högberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Körner, C., Leadley, P. W., Loreau, M., Minns, A., Mulder, C. P., O'Donovan, G., Otway, S. J., Pereira, J. S., Prinz, A., Read, D. J., Scherer-Lorenzen, M., Schulze, E. D., Siamantziouras, A. S. D., Spehn, E. M., Terry, A. C., Troumbis, A. Y., Woodward, F. I., Yachi, S., and Lawton, J. H. (1999). Plant diversity and productivity experiments in european grasslands. *Science*, 286(5442):1123–1127.

Heemsbergen, D. A., Berg, M. P., Loreau, M., van Hal, J. R., Faber, J. H., and Verhoef, H. A. (2004). Biodiversity effects on soil processes explained by interspecific functional dissimilarity. *Science*, 306:1019–1020.

Helmus, M. R., Savage, K., Diebel, M. W., Maxted, J. T., and Ives, A. R. (2007). Separating the determinants of phylogenetic community structure. *Ecology Letters*, 10(10):917–925.

Hendrickx, F., Maelfait, J., Wingerden, W. V., Schweiger, O., Speelmans, M., Aviron, S., Augenstein, I., Billeter, R., Bailey, D., Bukacek, R., Burel, F., Diekotter, T. I. M., Dirksen, J., Herzog, F., Liira, J., Roubalova, M., Vandomme, V., and Bugter, R. O. B. (2007). How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *Journal of Applied Ecology*, 44(2):340–351.

Herms, D. A. and Mattson, W. J. (1992). The dilemma of plants: to grow or defend. *The Quarterly Review of Biology*, 67(3):283.

Hewitt, A. E. (1998). *New Zealand Soil Classification*. Manaaki Whenua Press, Lincoln, New Zealand.

Hillebrand, H. and Matthiessen, B. (2009). Biodiversity in a complex world: consolidation and progress in functional biodiversity research. *Ecology Letters*, 12(12):1405–1419.

Hobbs, R. J., Yates, S., and Mooney, H. A. (2007). Long-term data reveal complex dynamics in grassland in relation to climate and disturbance. *Ecological Monographs*, 77(4):545–568.

Hocking, P. and Jeffery, S. (2004). Cluster-root production and organic anion exudation in a group of old-world lupins and a new-world lupin. *Plant and Soil*, 258(1):135–150.

Hodgson, J. G., Thompson, J., Wilson, P. J., and Bogaard, A. (1998). Does biodiversity determine ecosystem function? the Ecotron experiment reconsidered. *Functional Ecology*, 12:843–848.

Hodgson, J. G., Wilson, P. J., Hunt, H. R., Grime, J. P., and Thompson, K. (1999). Allocating C-S-R plant functional types: a soft approach to a hard problem. *Oikos*, 85:282–294.

Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, 4:1–23.

Holling, C. S. and Meffe, G. K. (1996). Command and control and the pathology of natural resource management. *Conservation Biology*, 10(2):328–337.

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J., and Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, 75(1):3–35.

Hooper, D. U., Solan, M., Symstad, A. J., Díaz, S., Gessner, M. O., Buchmann, N., Degrange, V., Grime, J. P., Hulot, F., Mermillod-Blondin, F., Roy, J., Spehn, E., and van Peer, L. (2002). Species diversity, functional diversity, and ecosystem functioning. In Loreau, M., Naeem, S., and Inchausti, P., editors, *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives*, pages 195–208. Oxford University Press, UK.

Hooper, D. U. and Vitousek, P. M. (1997). The effects of plant composition and diversity on ecosystem processes. *Science*, 277:1302–1305.

Hopf, F. A. and Brown, J. H. (1986). The bull's-eye method for testing randomness in ecological communities. *Ecology*, 67(5):1139–1155.

Hothorn, T., Bretz, F., and Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, 50(3):346–363.

Hugues, J. G. (1975). *A Study of the Grazing Preference of Sheep on Developed and Undeveloped Grassland at a High-Country Site*. MSc thesis, Lincoln College, University of Canterbury, Lincoln, New Zealand.

Huston, M. A. (1997). Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, 110:449–460.

Huston, M. A., Aarssen, L. W., Austin, M. P., Cade, B. S., Fridley, J. D., Garnier, E., Grime, J. P., Hodgson, J., Lauenroth, W. K., Thompson, K., Vandermeer, J. H., Wardle, D. A., Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M. C., Diemer, M., Dimitrakopoulos, P. G., Finn, J. A., Freitas, H., Giller, P. S., Good, J., Harris, R., Hogberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Korner, C., Leadley, P. W., Loreau, M., Minns, A., Mulder, C. P. H., O'Donovan, G., Otway, S. J., Pereira, J. S., Prinz, A., Read, D. J., Scherer-Lorenzen, M., Schulze, E. D., Siamantziouras, A. S. D., Spehn, E., Terry, A. C., Troumbis, A. Y., Woodward, F. I., Yachi, S., and Lawton, J. H. (2000). No consistent effect of plant diversity on productivity. *Science*, 289(5483):1255a.

Huston, M. A. and McBride, A. C. (2002). Evaluating the relative strengths of biotic versus abiotic controls on ecosystem processes. In Loreau, M., Naeem, S., and Inchausti, P., editors, *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives*, pages 47–60. Oxford University Press, UK.

Hutchinson, K. J. and King, K. L. (1980). The effects of sheep stocking level on invertebrate abundance, biomass and energy utilization in a temperate, sown grassland. *Journal of Applied Ecology*, 17(2):369–387.

Ingram, T. and Shurin, J. B. (2009). Trait-based assembly and phylogenetic structure in northeast pacific rockfish assemblages. *Ecology*, 90(9):2444–2453.

Israel, D. W. (1987). Investigation of the role of phosphorus in symbiotic dinitrogen fixation. *Plant Physiology*, 84(3):835–840.

IUCN (2007). World database on protected areas. Technical report, IUCN, Washington, DC, USA.

Jackson, L. E., Pascual, U., Brussaard, L., de Ruiter, P., and Bawa, K. S. (2007a). Biodiversity in agricultural landscapes: investing without losing interest. *Agriculture, Ecosystems & Environment*, 121(3):193–195.

Jackson, L. E., Pascual, U., and Hodgkin, T. (2007b). Utilizing and conserving agrobiodiversity in agricultural landscapes. *Agriculture, Ecosystems & Environment*, 121(3):196–210.

Jackson, R. B., Banner, J. L., Jobbagy, E. G., Pockman, W. T., and Wall, D. H. (2002). Ecosystem carbon loss with woody plant invasion of grasslands. *Nature*, 418:623–626.

Jax, K. (2005). Function and "functioning" in ecology: what does it mean? *Oikos*, 111(3):641–648.

Jaynes, E. T. (2003). *Probability Theory: The Logic of Science*. Cambridge University Press, Cambridge, UK.

Johnson, D. E., Johnson, K. A., Ward, G. M., and Branine, M. E. (2000). Ruminant and other animals. In Kahill, M. A. K., editor, *Atmospheric Methane: Its Role in the Global Environment*, pages 112–133. Springer-Verlag, Berlin, Germany.

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61(1):65.

Jones, M. B. and Alison, D. (2004). Carbon sequestration in temperate grassland ecosystems and the influence of management, climate and elevated CO_2. *New Phytologist*, 164(3):423–439.

Jöreskog, K. G. (1969). A general approach to confirmatory maximum likelihood factor analysis. *Psychometrika*, 34(2):183–202.

Kahmen, A., Perner, J., Audorff, V., Weisser, W., and Buchmann, N. (2005). Effects of plant diversity, community composition and environmental parameters on productivity in montane European grasslands. *Oecologia*, 142:606–615.

Kaiser, J. (1997). A nasty brew from pasture fires. *Science*, 277(5330):1205a–.

Kanowski, J., Catterall, C. P., Wardell-Johnson, G., Proctor, H., and Reis, T. (2003). Development of forest structure on cleared rainforest land in eastern Australia under different styles of reforestation. *Forest Ecology & Management*, 183:265–280.

Kareiva, P., Watts, S., McDonald, R., and Boucher, T. (2007). Domesticated nature: shaping landscapes and ecosystems for human welfare. *Science*, 316(5833):1866–1869.

Keddy, P. A. (1990). The use of functional as opposed to phylogenetic systematics: a first step in predictive community ecology. In Kawano, S., editor,

Biological Approaches and Evolutionary Trends in Plants. Academic Press, London, UK.

Keddy, P. A. (1992). Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*, 3:157–164.

Keddy, P. A. and Weiher, E. (1999). Introduction: The scope and goals of research on assembly rules. In Weiher, E. and Keddy, P. A., editors, *Ecological Assembly Rules: Perspectives, Advances, Retreats*, pages 1–22. Cambridge University Press, Cambridge, USA.

King, W. M. and Wilson, J. B. (2006). Differentiation between native and exotic plant species from a dry grassland: fundamental responses to resource availability, and growth rates. *Austral Ecology*, 31(8):996–1004.

Kinzig, A. P., Pacala, S. W., and Tilman, D. (2002). *Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions*. Princeton University Press, NJ, USA.

Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., Poschlod, P., van Groenendael, J. M., Klime, L., Klime, J., ová S Klotz, Rusch, G. M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuytm, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J. G., Jackel, A. K., Kühn, I., Kunzmann, D., Ozinga, W. A., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H. J., Tackenberg, O., Wilmann, B., Cornelissen, J. H. C., Eriksson, O., Garnier, E., and Peco, B. (2008). The LEDA traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology*, 96(6):1266–1274.

Kraft, N. and Ackerly, D. (2010). Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. *Ecological Monographs*, 80:401–422.

Kraft, N. J. B., Valencia, R., and Ackerly, D. D. (2008). Functional traits and niche-based tree community assembly in an Amazonian forest. *Science*, 322(5901):580–582.

Kramer, M. (2005). R^2 statistics for mixed models. *Proceedings of the Conference on Applied Statistics in Agriculture*, 17:148–160.

Krebs, J. R., Wilson, J. D., Bradbury, R. B., and Siriwardena, G. M. (1999). The second silent spring? *Nature*, 400(6745):611–612.

Kremen, C., Williams, N. M., Aizen, M. A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S. G., Roulston, T., Steffan-Dewenter, I., Vazquez, D. P., Winfree, R., Adams, L., Crone, E. E., Greenleaf, S. S., Keitt, T. H., Klein, A., Regetz, J., and Ricketts, T. H. (2007). Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters*, 10(4):299–314.

Kremen, C., Williams, N. M., and Thorp, R. W. (2002). Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences (USA)*, 99(26):16812–16816.

Krusell, L., Krause, K., Ott, T., Desbrosses, G., Kramer, U., Sato, S., Nakamura, Y., Tabata, S., James, E. K., Sandal, N., Stougaard, J., Kawaguchi, M., Miyamoto, A., Suganuma, N., and Udvardi, M. K. (2005). The sulfate transporter SST1 is crucial for symbiotic nitrogen fixation in *Lotus japonicus* root nodules. *Plant Cell*, 17(5):1625–1636.

Kruskal, J. B. (1964). Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika*, 29:1–27.

Laliberté, E. (2009). *metacor: Meta-analysis with correlation coefficients as effect sizes. R package version 1.0-1.* The Comprehensive Archive Network (CRAN), Vienna, Austria.

Laliberté, E. and Shipley, B. (2010). *FD: Measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-9.* The Comprehensive R Archive Network (CRAN), Vienna, Austria.

Lambers, H., Chapin, F. S., and Pons, T. L. (2008a). *Plant Physiological Ecology*. Springer, New York, USA, second edition edition.

Lambers, H. and Poorter, H. (1992). Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Advances in Ecological Research*, 23:187–261.

Lambers, H., Raven, J. A., Shaver, G. R., and Smith, S. E. (2008b). Plant nutrient-acquisition strategies change with soil age. *Trends in Ecology & Evolution*, 23(2):95–103.

Landcare Research (2008). Ecological traits of New Zealand flora. Electronic database.

Landsberg, J. (1999). Response and effect - different reasons for classifying plant functional types under grazing. In Eldridge, D. and Freudenberger, D., editors, *People and Rangelands: Building the Future*, pages 911–915. Proceedings of the VI International Rangeland Congress, Townsville, Australia.

Landsberg, J., O'Connor, T., and Freudenberger, D. (1999). The impacts of livestock grazing on biodiversity in natural ecosystems. In Jung, H. J. G. and Fahey, G. C., editors, *Nutritional Ecology of Herbivores*, pages 752–777. American Society of Animal Science, IL, USA.

Larsen, T. H., Williams, N. M., and Kremen, C. (2005). Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters*, 8(5):538–547.

Lauenroth, W. K. (2000). Methods of estimating belowground net primary production. In Sala, O. E., Jackson, R. B., Mooney, H. A., and Howarth, R. W., editors, *Methods in Ecosystem Science*, pages 58–71. Springer, New York, USA.

Laughlin, D. C., Leppert, J. J., Moore, M. M., and Sieg, C. H. (2010). A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology*, 24(3):493–501.

Laurance, W. F., Albernaz, A. K. M., Fearnside, P. M., Vasconcelos, H. L., and Ferreira, L. V. (2004). Deforestation in Amazonia. *Science*, 304:1109.

Lavorel, S., Díaz, S., Cornelissen, J. H. C., Garnier, E., Harrison, S. P., McIntyre, S., Pausas, J. G., Pérez-Harguindeguy, N., Roumet, C., and Urcelay, C. (2007). Plant functional types: are we getting any closer to the Holy Grail? In Canadell, J. G., Pataki, D., and Pitelka, L., editors, *Terrestrial Ecosystems in a Changing world*, The IGBP Series, pages 149–160. Springer-Verlag, Berlin.

Lavorel, S. and Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, 16(5):545–556.

Lavorel, S., Grigulis, K., McIntyre, S., Williams, N. S. G., Garden, D., Dorrough, J., Berman, S., Quétier, F., Thébault, A., and Bonis, A. (2008). Assessing functional diversity in the field - methodology matters! *Functional Ecology*, 22(1):134–147.

Lavorel, S., McIntyre, S., Landsberg, J., and Forbes, T. D. A. (1997). Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology and Evolution*, 12(12):474–478.

Lawler, S. P., Armesto, J. J., and Kareiva, P. (2002). How relevant to conservation are studies linking biodiversity and ecosystem functioning? In Kinzing, A. P., Pacala, S. W., and Tilman, D., editors, *Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions*, pages 294–313. Princeton University Press, NJ, USA.

Lawton, J. H. and Brown, V. K. (1993). Redundancy in ecosystems. In Schulze, E. D. and Mooney, H. A., editors, *Biodiversity and Ecosystem Function*, pages 255–270. Springer-Verlag, Berlin, Germany.

Le Maitre, D. C., Milton, S. J., Jarmain, C., Colvin, C. A., Saayman, I., and Vlok, J. H. J. (2007). Linking ecosystem services and water resources: landscape-scale hydrology of the Little Karoo. *Frontiers in Ecology and the Environment*, 5(5):261–270.

Lebrija-Trejos, E., Pérez-García, E. A., Meave, J. A., Bongers, F., and Poorter, L. (2010). Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology*, 91(2):386–398.

Lecerf, A. and Chauvet, E. (2008). Intraspecific variability in leaf traits strongly affects alder leaf decomposition in a stream. *Basic and Applied Ecology*, 9(5):598–605.

Leff, B., Ramankutty, N., and Foley, J. A. (2004). Geographic distribution of major crops across the world. *Global Biogeochemical Cycles*, 18:GB1009.

Legendre, P. and Anderson, M. J. (1999). Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs*, 69(1):1–24.

Legendre, P., Borcard, D., and Peres-Neto, P. (2005). Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs*, 75:435–450.

Legendre, P. and Legendre, L. (1998). *Numerical Ecology*. Elsevier Science, Amsterdam, Netherlands, 2nd english edition.

Leishman, M. R., Haslehurst, T., Ares, A., and Baruch, Z. (2007). Leaf trait relationships of native and invasive plants: community- and global-scale comparisons. *New Phytologist*, 176(3):635–643.

Leps, J. (2004). What do the biodiversity experiments tell us about consequences of plant species loss in the real world? *Basic and Applied Ecology*, 5(6):529–534.

Levene, H. (1960). Robust tests for equality of variances. In Olkin, S. G., Hoeffding, W., Madow, W. G., and Mann, H. B., editors, *Contributions to Probability and Statistics*, pages 278–292. Stanford University Press, California, USA.

Lingoes, J. C. (1971). Some boundary conditions for a monotone analysis of symmetric matrices. *Psychometrika*, 36:195–203.

Linklater, W. and Cameron, E. (2000). Tests for cooperative behaviour between stallions. *Animal Behaviour*, 60:731–743.

Linklater, W. and Cameron, E. (2009). Social dispersal but with philopatry reveals incest avoidance in a polygynous ungulate. *Animal Behaviour*, 77(5):1085–1093.

Lockwood, J. L., Moulton, M. P., and Anderson, S. K. (1993). Morphological assortment and the assembly of communities of introduced passeriforms on oceanic islands: Tahiti versus Oahu. *American Naturalist*, 141(3):398–408.

Loreau, M. (2000). Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos*, 91:3–17.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., Hooper, D. U., Huston, M. A., Raffaelli, D., Schmid, B., Tilman, D., and Wardle, D. A. (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, 294:804–808.

Louault, F., Pillar, V., Aufrère, J., Garnier, E., and Soussana, J. (2005). Plant traits and functional types in response to reduced disturbance in a semi-natural grassland. *Journal of Vegetation Science*, 16(2):151–160.

Luck, G., Harrington, R., Harrison, P., Kremen, C., Berry, P., Bugter, R., Dawson, T., de Bello, F., Diaz, S., Feld, C., Haslett, J., Hering, D., Kontogianni, A., Lavorel, S., Rounsevell, M., Samways, M., Sandin, L., Settele, J., Sykes, M., van den Hove, S., Vandewalle, M., and Zobel, M. (2009).

Quantifying the contribution of organisms to the provision of ecosystem services. *BioScience*, 59(3):223–235.

Ludecke, T. E. (1962). Formulation of a rational fertilizer programme in tussock country. *Proceedings of the New Zealand Grassland Association*, 24:29–41.

Ludwig, D., Walker, B., and Holling, C. S. (1997). Sustainability, stability, and resilience. *Conservation Ecology*, 1(1):7.

Luscier, J. D., Thompson, W. L., Wilson, J. M., Gorham, B. E., and Dragut, L. D. (2006). Using digital photographs and object-based image analysis to estimate percent ground cover in vegetation plots. *Frontiers in Ecology and the Environment*, 4(8):408–413.

MacArthur, R. H. and Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist*, 101:377–385.

Maire, V., Gross, N., da Silveira Pontes, L., Picon-Cochard, C., and Soussana, J. (2009). Trade-off between root nitrogen acquisition and shoot nitrogen utilization across 13 co-occurring pasture grass species. *Functional Ecology*, 23(4):668–679.

Marks, C. O. and Lechowicz, M. J. (2006). Alternative designs and the evolution of functional diversity. *American Naturalist*, 167(1):55–66.

Marks, C. O. and Muller-Landau, H. C. (2007). Comment on "From plant traits to plant communities: A statistical mechanistic approach to biodiversity". *Science*, 316(5830):1425c.

Mason, N., Lanoiselée, C., Mouillot, D., Irz, P., and Argillier, C. (2007). Functional characters combined with null models reveal inconsistency in mechanisms of species turnover in lacustrine fish communities. *Oecologia*, 153(2):441–452.

Mason, N. W. H., MacGillivray, K., Steel, J. B., and Wilson, J. B. (2003). An index of functional diversity. *Journal of Vegetation Science*, 14(4):571–578.

Matson, P. A., Parton, W. J., Power, G. A., and Swift, M. J. (1997). Agricultural intensification and ecosystem properties. *Science*, 277:504–509.

Matson, P. A. and Vitousek, P. M. (2006). Agricultural intensification: will land spared from farming be land spared for nature? *Conservation Biology*, 20(3):709–710.

Mattison, E. H. A. and Norris, K. (2005). Bridging the gaps between agricultural policy, land-use and biodiversity. *Trends in Ecology & Evolution*, 20(11):610–616.

May, R. M. (1977). Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature*, 269(5628):471–477.

Mayfield, M. M., Ackerly, D., and Daily, G. C. (2006). The diversity and conservation of plant reproductive and dispersal functional traits in human-dominated tropical landscapes. *Journal of Ecology*, 94(3):522–536.

Mayfield, M. M., Boni, M. F., Daily, G. C., and Ackerly, D. (2005). Species and functional diversity of native and human-dominated plant communities. *Ecology*, 86(9):2365–2372.

Mayfield, M. M. and Levine, J. M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, 13:1085–1092.

McAllister, R. R. J., Gordon, I. J., Janssen, M. A., and Abel, N. (2006). Pastoralists' responses to variation of rangeland resources in time and space. *Ecological Applications*, 16(2):572–583.

McArdle, B. H. and Anderson, M. J. (2001). Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology*, 82(1):290–297.

McGill, B. J. (2006). A renaissance in the study of abundance. *Science*, 314:770–772.

McGill, B. J., Enquist, B. J., Weiher, E., and Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21(4):178–185.

McGill, B. J. and Nekola, J. C. (2010). Mechanisms in macroecology: AWOL or purloined letter? towards a pragmatic view of mechanism. *Oikos*, 119(4):591–603.

McGlone, M. S. (2001). The origin of native grasslands of southeastern south island in relation to pre-human woody ecosystems. *New Zealand Journal of Ecology*, 25(1):1–15.

McIntyre, S. (2008). The role of plant leaf attributes in linking land use to ecosystem function in temperate grassy vegetation. *Agriculture, Ecosystems & Environment*, 128(4):251–258.

McIntyre, S. and Lavorel, S. (2007). A conceptual model of land use effects on the structure and function of herbaceous vegetation. *Agriculture, Ecosystems & Environment*, 119(1-2):11–21.

McKane, R. B., Johnson, L. C., Shaver, G. R., Nadelhoffer, K. J., Rastetter, E. B., Fry, B., Giblin, A. E., Kielland, K., Kwiatkowski, B. L., Laundre, J. A., and Murray, G. (2002). Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature*, 415(6867):68–71.

McNaughton, S. J. (1983). Compensatory plant growth as a response to herbivory. *Oikos*, 40(3):329–336.

McNaughton, S. J., Banyikwa, F. F., and McNaughton, M. M. (1997). Promotion of the cycling of diet-enhancing nutrients by African grazers. *Science*, 278:1798–1800.

McNaughton, S. J., Banyikwa, F. F., and McNaughton, M. M. (1998). Root biomass and productivity in a grazing ecosystem: the Serengeti. *Ecology*, 79(2):587–592.

McNaughton, S. J., Milchunas, D. G., and Frank, D. A. (1996). How can net primary productivity be measured in grazing ecosystems? *Ecology*, 77(3):974–977.

McNaughton, S. J., Oesterheld, M., Frank, D. A., and Williams, K. J. (1989). Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature*, 341:142–144.

Meentemeyer, R. and Moody, A. (2000). Rapid sampling of plant species composition for assessing vegetation patterns in rugged terrain. *Landscape Ecology*, 15(8):697–711.

Meier, C. L. and Bowman, W. D. (2008). Links between plant litter chemistry, species diversity, and below-ground ecosystem function. *Proceedings of the National Academy of Sciences*, 105(50):19780–19785.

Micheli, F. and Halpern, B. S. (2005). Low functional redundancy in coastal marine assemblages. *Ecology Letters*, 8:391–400.

Milchunas, D. G. and Lauenroth, W. K. (1993). A quantitative assessment of the effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs*, 63:327–366.

Millennium Ecosystem Assessment (2005a). Ecosystems and Human Well-Being: Desertification Synthesis. Technical report, World Resources Institute, Washington, DC, USA.

Millennium Ecosystem Assessment (2005b). Ecosystems and Human Well-Being: Synthesis. Technical report, Island Press, Washington, DC.

Minns, A., Finn, J. A., Hector, A., Caldeira, M. C., Joshi, J., Palmborg, C., Schmid, B., Scherer-Lorenzen, M., Spehn, E., Troumbis, A. Y., and

project, B. (2001). The functioning of european grassland ecosystems: potential benefits of biodiversity to agriculture. *Outlook on Agriculture*, 30(3):179–185.

Mokany, K., Ash, J., and Roxburgh, S. (2008). Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology*, 96(5):884–893.

Mokany, K. and Roxburgh, S. H. (2010). The importance of spatial scale for trait-abundance relations. *Oikos*, in press.

Moller, H., MacLeod, C. J., Haggerty, J., Rosin, C., Blackwell, G., Perley, C., Meadows, S., Weller, F., and Gradhohl, M. (2008). Intensification of New Zealand agriculture: implications for biodiversity. *New Zealand Journal of Agricultural Research*, 51:253–263.

Mooney, H. A. (2002). The debate on the role of biodiversity in ecosystem functioning. In Loreau, M., Naeem, S., and Inchausti, P., editors, *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives*, pages 12–17. Oxford University Press, UK.

Mouillot, D., Mason, W. H. N., Dumay, O., and Wilson, J. B. (2005). Functional regularity: a neglected aspect of functional diversity. *Oecologia*, 142(3):353–359.

Moulton, M. P. and Pimm, S. L. (1987). Morphological assortment in introduced Hawaiian passerines. *Evolutionary Ecology*, 1(2):113–124.

Myers, N. and Kent, J. (2003). New consumers: the influence of affluence on the environment. *Proceedings of the National Academy of Sciences (USA)*, 100(8):4963–4968.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403:853–858.

Müeller-Dombois, D. and Ellenberg, H. (2003). *Aims and Methods of Vegetation Ecology*. The Blackburn Press, New Jersey, USA.

Naeem, S. (1998). Species redundancy and ecosystem reliability. *Conservation Biology*, 12(1):39–45.

Naeem, S. and Li, S. (1997). Biodiversity enhances ecosystem reliability. *Nature*, 390:507–509.

Naeem, S., Thompson, L. J., Lawler, S. P., Lawton, J. H., and Woodfin, R. M. (1994). Declining biodiversity can alter the performance of ecosystems. *Nature*, 368:734–737.

Naeem, S. and Wright, J. P. (2003). Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters*, 6(6):567–579.

Naylor, R., Steinfeld, H., Falcon, W., Galloway, J., Smil, V., Bradford, E., Alder, J., and Mooney, H. (2005). Losing the links between livestock and land. *Science*, 310(5754):1621–1622.

Neill, C. (1992). Comparison of soil coring and ingrowth methods for measuring belowground production. *Ecology*, 73(5):1918–1921.

Nepstad, D. C., Verssimo, A., Alencar, A., Nobre, C., Lima, E., Lefebvre, P., Schlesinger, P., Potter, C., Moutinho, P., Mendoza, E., Cochrane, M., and Brooks, V. (1999). Large-scale impoverishment of Amazonian forests by logging and fire. *Nature*, 398(6727):505–508.

Norberg, J., Swaney, D. P., Dushoff, J., Lin, J., Casagrandi, R., and Levin, S. A. (2001). Phenotypic diversity and ecosystem functioning in changing environments: A theoretical framework. *Proceedings of the National Academy of Sciences (USA)*, 98(20):11376–11381.

Norton, D. A. (2000). Conservation biology and private land: shifting the focus. *Conservation Biology*, 14(5):1221–1223.

Norton, D. A., Espie, P. R., Murray, W., and Murray, J. (2006). Influence of pastoral management on plant biodiversity in a depleted short tussock grassland, Mackenzie Basin. *New Zealand Journal of Ecology*, 30(3):335–344.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G. L., Solymos, P., Stevens, M. H. H., and Wagner, H. (2010). *vegan: Community Ecology Package. R package version 1.17-0.* The Comprehensive R Archive Network (CRAN), Vienna, Austria.

Olff, H. and Ritchie, M. E. (1998). Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution*, 13(7):261–265.

Olivera, M., Tejera, N., Iribarne, C., Ocaña, A., and Lluch, C. (2004). Growth, nitrogen fixation and ammonium assimilation in common bean (*Phaseolus vulgaris*): effect of phosphorus. *Physiologia Plantarum*, 121(3):498–505.

Olson, J. S. (1963). Energy storage and the balance of producers and decomposers in ecological systems. *Ecology*, 44(2):322–331.

Pastor, J., Naiman, R. J., Dewey, B., and McInnes, P. (1988). Moose, microbes, and the boreal forest. *BioScience*, 38(11):770–777.

Pavoine, S., Vallet, J., Dufour, A., Gachet, S., and Daniel, H. (2009). On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos*, 118(3):391–402.

Pearson, S. M., Smith, A. B., and Turner, M. G. (1998). Forest patch size, land use, and mesic forest herbs in the French Broad River Basin, North Carolina. *Castanae*, 63:382–395.

Peat, H., Fitter, A., and Ford, H. (2008). Ecological database of the British Isles. Electronic database.

Peres-Neto, P. R. and Jackson, D. A. (2001). How well do multivariate data sets match? the advantages of a Procrustean superimposition approach over the Mantel test. *Oecologia*, 129(2):169–178.

Perrings, C., Jackson, L., Bawa, K., Brussaard, L., Brush, S., Gavin, T., Papa, R., Pascual, U., and Ruiter, P. D. (2006). Biodiversity in agricultural landscapes: saving natural capital without losing interest. *Conservation Biology*, 20(2):263–264.

Personeni, E. and Loiseau, P. (2004). How does the nature of living and dead roots affect the residence time of carbon in the root litter continuum? *Plant and Soil*, 267(1-2):129–141.

Petchey, O. L., Evans, K. L., Fishburn, I. S., and Gaston, K. J. (2007). Low functional diversity and no redundancy in British avian assemblages. *Journal of Animal Ecology*, 76(5):977–985.

Petchey, O. L. and Gaston, K. J. (2002). Functional diversity (FD), species richness and community composition. *Ecology Letters*, 5(3):402–411.

Petchey, O. L. and Gaston, K. J. (2006). Functional diversity: back to basics and looking forward. *Ecology Letters*, 9(6):741–758.

Peterson, G., Allen, C. R., and Holling, C. S. (1998). Ecological resilience, biodiversity, and scale. *Ecosystems*, 1:6–18.

Pimm, S. L. and Raven, P. (2000). Extinction by numbers. *Nature*, 403:843–845.

Pimm, S. L., Russell, G. J., Gittleman, J. L., and Brooks, T. M. (1995). The future of biodiversity. *Science*, 269(5222):347–350.

Pinheiro, J., Bates, D., and DebRoy, S. (2010). *nlme: Linear and Nonlinear Mixed Effects Models. R package 3.1.96.* The Comprehensive R Archive Network (CRAN), Vienna, Austria.

Pinheiro, J. C. and Bates, D. M. (2000). *Mixed-Effects Models in S and S-PLUS*. Springer, New York, USA.

Podani, J. (1999). Extending Gower's general coefficient of similarity to ordinal characters. *Taxon*, 48(2):331–340.

Poorter, H. and Bergkotte, M. (1992). Chemical composition of 24 wild species differing in relative growth rate. *Plant, Cell and Environment*, 15(2):221–229.

Poorter, H. and Remkes, C. (1990). Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia*, 83(4):553–559.

Prinzing, A., Reiffers, R., Braakhekke, W. G., Hennekens, S. M., Tackenberg, O., Ozinga, W. A., Schaminée, J. H. J., and van Groenendael, J. M. (2008). Less lineages – more trait variation: phylogenetically clustered plant communities are functionally more diverse. *Ecology Letters*, 11(8):809–819.

Prosser, C., Skinner, K., and Sedivec, K. (2003). Comparison of two techniques for monitoring vegetation on military lands. *Journal of Range Management*, 56(5):446–454.

Quested, H., Eriksson, O., Fortunel, C., and Garnier, É. (2007). Plant traits relate to whole-community litter quality and decomposition following land use change. *Functional Ecology*, 21(6):1016–1026.

Quétier, F., Lavorel, S., Thuiller, W., and Davies, I. (2007a). Plant-trait based modeling assessment of ecosystem-service sensitivity to land-use change. *Ecological Applications*, 17(8):2377–2386.

Quétier, F., Thébault, A., and Lavorel, S. (2007b). Plant traits in a state and transition framework as markers of ecosystem response to land-use change. *Ecological Monographs*, 77(1):33–52.

R Development Core Team (2010). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.

Rada, F. (2000). Deforestation impact on water dynamics in a Venezuelan Andean cloud forest. *Ambio*, 29(7):440–444.

Raich, J. W. and Tufekciogul, A. (2000). Vegetation and soil respiration: correlations and controls. *Biogeochemistry*, 48(1):71–90.

Ramankutty, N., Evan, A. T., Monfreda, C., and Foley, J. A. (2008). Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. *Global Biogeochemical Cycles*, 22:GB1003.

Rao, C. R. (1982). Diversity and dissimilarity coefficients – a unified approach. *Theoretical Population Biology*, 21(1):24–43.

Reich, P. B., Walters, M. B., and Ellsworth, D. S. (1992). Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs*, 62(3):365.

Reich, P. B., Walters, M. B., and Ellsworth, D. S. (1997). From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences (USA)*, 94(25):13730–13734.

Reiss, J., Bridle, J. R., Montoya, J. M., and Woodward, G. (2009). Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology & Evolution*, 24(9):505–514.

Ricklefs, R. E. and Travis, J. (1980). A morphological approach to the study of avian community organization. *Auk*, 97:321–338.

Ricotta, C. (2005). A note on functional diversity measures. *Basic and Applied Ecology*, 6(5):479–486.

Robertson, A. I. (2000). The gaps between ecosystem ecology and industrial agriculture. *Ecosystems*, 3:413–418.

Robertson, G. P. and Swinton, S. M. (2005). Reconciling agricultural productivity and environmental integrity: a grand challenge for agriculture. *Frontiers in Ecology and the Environment*, 3(1):38–46.

Rook, A. J. and Tallowin, J. R. B. (2003). Grazing and pasture management for biodiversity benefit. *Animal Research*, 52:181–189.

Rosenfeld, J. S. (2002). Functional redundancy in ecology and conservation. *Oikos*, 98(1):156–162.

Rosenthal, J. and Kotanen, P. (1994). Terrestrial plant tolerance to herbivory. *Trends in Ecology & Evolution*, 9(4):145–148.

Rosenzweig, C., Casassa, G., Karoly, D. J., Imeson, A., Liu, C., Menzel, A., Rawlins, S., Root, T. L., Séguin, B., and Tryjanowski, P. (2007). Assessment of observed changes and responses in natural and managed systems. In Parry, M. L., Canziani, O. F., Palutikof, J. P., van der Linden, P. J., and Hanson, C. E., editors, *Climate Change 2007: Impacts, Adaptations and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC)*, pages 79–131. Cambridge University Press, UK.

Roxburgh, S. H. and Mokany, K. (2007). Comment on "From plant traits to plant communities: A statistical mechanistic approach to biodiversity". *Science*, 316(5830):1425b.

Roxburgh, S. H. and Mokany, K. (2010). On testing predictions of species relative abundance from maximum entropy optimisation. *Oikos*, 119(4):583–590.

Ryser, P. (1996). The importance of tissue density for growth and life span of leaves and roots: a comparison of five ecologically contrasting grasses. *Functional Ecology*, 10(6):717–723.

Ryser, P. and Aeschlimann, U. (1999). Proportional dry-mass content as an underlying trait for the variation in relative growth rate among 22 Eurasian populations of *Dactylis glomerata* s.l. *Functional Ecology*, 13(4):473–482.

Ryser, P. and Lambers, H. (1995). Root and leaf attributes accounting for the performance of fast- and slow-growing grasses at different nutrient supply. *Plant and Soil*, 170(2):251–265.

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, L., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Puff, N. L., Sykes, M. T., Walker, B. H., Walker, M., and Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. *Science*, 287:1770–1774.

Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V., and Woolmer, G. (2002). The human footprint and the last of the wild. *BioScience*, 52(10):891–904.

Sanderson, M. A. (2005). Plant species diversity: management implications for temperate pasture production. In Bhatti, J., Lal, R., Price, M., and Apps, M., editors, *Climate change and managed ecosystems*, pages 149–161. CRC Press, Boca Raton, Florida, USA.

Sanderson, M. A., Goslee, S. C., Soder, K. J., and Skinner, R. H. (2007). Plant species diversity, ecosystem function, and pasture management - a perspective. *Canadian Journal of Plant Science*, 87(479-487).

Sanderson, M. A., Skinner, R. H., Barker, D. J., Edwards, G. R., Tracy, B. F., and Wedin, D. A. (2004). Plant species diversity and management of temperate forage and grazing land ecosystems. *Crop Science*, 44(4):1132–1144.

Sanderson, M. A., Soder, K. J., Muller, L. D., Klement, K. D., Skinner, R. H., and Goslee, S. C. (2005). Forage mixture productivity and botanical composistion in pastures grazed by dairy cattle. *Agronomy Journal*, 87(5):1465–1471.

Sasaki, T., Okayasu, T., Jamsran, U., and Takeuchi, K. (2008). Threshold changes in vegetation along a grazing gradient in Mongolian rangelands. *Journal of Ecology*, 96(1):145–154.

Schaffers, A. P. (2002). Soil, biomass, and management of semi-natural vegetation. Part I. Interrelationships. *Plant Ecology*, 158:229–246.

Scheffer, M., Carpenter, S. R., Foley, J. A., Folke, C., and Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, 413:591–596.

Scherer, H. W. and Lange, A. (1996). N_2 fixation and growth of legumes as affected by sulphur fertilization. *Biology and Fertility of Soils*, 23(4):449–453.

Schimper, A. F. W. (1898). *Pflanzengeographie auf Physiologischer Grundlage*. G. Fischer.

Schläpfer, F., Pfisterer, A. B., and Schmid, B. (2005). Non-random species extinction and plant production: implications for ecosystem functioning. *Journal of Applied Ecology*, 42(1):13–24.

Schulze, J., Adgo, E., and Merbach, W. (1999). Carbon costs associated with N_2 fixation in *Vicia faba* l. and *Pisum sativum* l. over a 14-day period. *Plant Biology*, 1(6):625–631.

Schulze, R. (2004). *Meta-Analysis: A Comparison of Approaches*. Hogrefe & Huber, Göttingen, Germany.

Scott, D. (1970). Relative growth rates under controlled temperatures of some New Zealand indigenous and introduced grasses. *New Zealand Journal of Botany*, 8:369–379.

Scott, D. (1989). Description of vegetation using visual ranking of species. *New Zealand Journal of Ecology*, 12:77–88.

Scott, D. (1999). Sustainability of New Zealand high-country pastures under contrasting development inputs. 1. Site, and shoot nutrients. *New Zealand Journal of Agricultural Research*, 42:365–383.

Scott, D. (2000a). Fertiliser and grazing rejuvenation of fescue tussock grassland. *New Zealand Journal of Agricultural Research*, 43:481–490.

Scott, D. (2000b). Sustainability of New Zealand high-country pastures under contrasting development inputs. 2. Soil inorganic components. *New Zealand Journal of Agricultural Research*, 43(1):101–125.

Scott, D. (2000c). Sustainability of New Zealand high-country pastures under contrasting development inputs. 3. Sheep carrying capacity. *New Zealand Journal of Agricultural Research*, 43(2):175–185.

Scott, D. (2000d). Sustainability of New Zealand high-country pastures under contrasting development inputs. 4. Organic matter components. *New Zealand Journal of Agricultural Research*, 43(3):387–414.

Scott, D. (2000e). Sustainability of New Zealand high-country pastures under contrasting development inputs. 5. Nutrient pools and balances. *New Zealand Journal of Agricultural Research*, 43(3):415–438.

Scott, D. (2000f). Sustainability of New Zealand high-country pastures under contrasting development inputs. 6. Fertiliser efficiency. *New Zealand Journal of Agricultural Research*, 43(4):525–532.

Scott, D. (2001). Sustainability of New Zealand high-country pastures under contrasting development inputs. 7. Environmental gradients, plant species selection, and diversity. *New Zealand Journal of Agricultural Research*, 44:59–90.

Scott, D. (2002). Sustainability of New Zealand high-country pastures under contrasting development inputs. 8. Modelling sheep carrying capacity. *New Zealand Journal of Agricultural Research*, 45:151–163.

Scott, D. (2007). Sustainability of New Zealand high-country pastures under contrasting development inputs. 9. Vegetation dynamics. *New Zealand Journal of Agricultural Research*, 50:396–406.

Seefeldt, S. and Booth, D. (2006). Measuring plant cover in sagebrush steppe rangelands: A comparison of methods. *Environmental Management*, 37(5):703–711.

Shannon, C. E. and Weaver, W. (1949). *The Mathemetical Theory of Communication*. Chicago University Press, Urbana, IL.

Sheil, D., Ducey, M. J., Sidiyasa, K., and Samsoedin, I. (2003). A new type of sample unit for the efficient assessment of diverse tree communities in complex forest landscapes. *Journal of Tropical Forest Science*, 15:117–135.

Shepard, R. N. (1962). The analysis of proximities: Multidimensional scaling with an unknown distance function, I. *Psychometrika*, 27(2):125–140.

Shipley, B. (2006). Net assimilation rate, specific leaf area and leaf mass ratio: which is most closely correlated with relative growth rate? A meta-analysis. *Functional Ecology*, 20(4):565–574.

Shipley, B. (2009a). Confirmatory path analysis in a generalized multilevel context. *Ecology*, 90(2):363–368.

Shipley, B. (2009b). Limitations of entropy maximization in ecology: a reply to Haegeman and Loreau. *Oikos*, 118(1):152–159.

Shipley, B. (2009c). Trivial and non-trivial applications of entropy maximization in ecology: Shipley's reply. *Oikos*, 118(8):1279–1280.

Shipley, B. (2010a). Community assembly, natural selection and maximum entropy models. *Oikos*, 119(4):604–609.

Shipley, B. (2010b). *From Plant Traits to Vegetation Structure: Chance and Selection in the Assembly of Ecological Communities*. Cambridge University Press, Cambridge, UK.

Shipley, B. (2010c). Inferential permutation tests for maximum entropy models in ecology. *Ecology*, in press.

Shipley, B., Laughlin, D., Sonnier, G., and Otfinowski, R. (2010). A strong test of a maximum entropy model of trait-based community assembly. *Ecology*, in press.

Shipley, B., Lechowicz, M. J., Wright, I., and Reich, P. B. (2006a). Fundamental trade-offs generating the worldwide leaf economics spectrum. *Ecology*, 87(3):535–541.

Shipley, B., Vile, D., and Garnier, E. (2007). Response to comments on "From plant traits to plant communities: A statistical mechanistic approach to biodiversity". *Science*, 316(5830):1425d.

Shipley, B., Vile, D., and Garnier, É. (2006b). From plant traits to plant communities: a statistical mechanistic approach to biodiversity. *Science*, 314:812–814.

Shugart, H. H. (1997). Plant and ecosystem functional types. In Smith, T. M., Shugart, H. H., and Woodward, F. I., editors, *Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change*, pages 20–43. Cambridge University Press, Cambridge, UK.

Silverman, B. W. (1986). *Density Estimation*. Chapman and Hall, London, UK.

Silvertown, J. (2004). Plant coexistence and the niche. *Trends in Ecology & Evolution*, 19(11):605–611.

Sims, D., Seemann, J., and Luo, Y. (1998). Elevated CO_2 concentration has independent effects on expansion rates and thickness of soybean leaves across light and nitrogen gradients. *Journal of Experimental Botany*, 49(320):583–591.

Six, J., Frey, S. D., Thiet, R. K., and Batten, K. M. (2006). Bacterial and fungal contributions to carbon sequestration in agroecosystems. *Soil Science Society of America Journal*, 70(2):555.

Smithson, M. and Verkuilen, J. (2006). A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. *Psychological Methods*, 11(1):54–71.

Sonnier, G., Navas, M. L., Fayolle, A., and Shipley, B. (2010a). A novel method to identify plant traits that determine community structure: a test in herbaceous plant communities under contrasted land use regimes. In preparation.

Sonnier, G., Shipley, B., and Navas, M. L. (2010b). Plant traits, species pools and the prediction of relative abundances in plant communities: a maximum entropy approach. *Journal of Vegetation Science*, 21:318–331.

Soussana, J., Loiseau, P., Vuichard, N., Ceschia, E., Balesdent, J., Chevallier, T., and Arrouays, D. (2004). Carbon cycling and sequestration opportunities in temperate grasslands. *Soil Use and Management*, 20(2):219–230.

Spehn, E. M., Hector, A., Joshi, J., Scherer-Lorenzen, M., Schmid, B., Bazeley-White, E., Beierkuhnlein, C., Caldeira, M. C., Diemer, M., Dimitrakopoulos, P. G., Finn, J. A., Freitas, H., Giller, P. S., Good, J., Harris, R., gberg, P., Huss-Danell, K., Jumpponen, A., Koricheva, J., Leadley, P. W., Loreau, M., Minns, A., Mulder, C. P. H., Donovan, G., Otway, S. J., Palmborg, C., Pereira, J. S., Pfisterer, A. B., Prinz, A., Read, D. J., Schulze, E. D., Siamantziouras, A. S. D., Terry, A. C., Troumbis, A. Y., Woodward, F. I., Yachi, S., and Lawton, J. H. (2005). Ecosystem effects of biodiversity manipulations in European grasslands. *Ecological Monographs*, 75(1):37–63.

Sprent, J. I. (1999). Nitrogen fixation and growth of non-crop legume species in diverse environments. *Perspectives in Plant Ecology, Evolution and Systematics*, 2(2):149–162.

Srivastava, D. S. and Vellend, M. (2005). Biodiversity-ecosystem function research: is it relevant to conservation? *Annual Review of Ecology and Systematics*, 36:267–294.

Stohlgren, T. J., Bull, K. A., and Otsuki, Y. (1998). Comparison of rangeland vegetation sampling techniques in the Central Grasslands. *Journal of Range Management*, 51(2):164–172.

Stubbs, W. J. and Wilson, J. B. (2004). Evidence for limiting similarity in a sand dune community. *Journal of Ecology*, 92(4):557–567.

Suding, K. N., Goldberg, D. E., and Hartman, K. M. (2003). Relationships among species traits: separating levels of response and identifying linkages to abundance. *Ecology*, 84(1):1–16.

Suding, K. N., Lavorel, S., Chapin, F. S., Cornelissen, J. H. C., Diaz, S., Garnier, E., Goldberg, D., Hooper, D. U., Jackson, S. T., and Navas, M. (2008). Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology*, 14(5):1125–1140.

Swenson, N. G., Enquist, B. J., Pither, J., Thompson, J., and Zimmermann, J. K. (2006). The problem and promise of scale dependency in community phylogenetics. *Ecology*, 87(10):2418–2424.

Swift, M. J. and Anderson, J. M. (1993). Biodiversity and ecosystem function in agricultural systems. In Schulze, E. D. and Mooney, H. A., editors, *Biodiversity and Ecosystem Function*, pages 15–41. Springer-Verlag, Berlin, Germany.

Symstad, A. J., Chapin, F. S., Wall, D. H., Gross, K. L., Huenneke, L. F., Mittelbach, G. G., Peters, D. P. C., and Tilman, D. (2003). Long-term and large-scale perspectives on the relationship between biodiversity and ecosystem functioning. *BioScience*, 53(1):89–98.

Symstad, A. J., Wienk, C. L., and Thorstenson, A. D. (2008). Precision, repeatability, and efficiency of two canopy-cover estimate methods in Northern Great Plains vegetation. *Rangeland Ecology & Management*, 61(4):419–429.

Syversten, J. P., LLoyd, J., McConchie, C., Kriedemann, P. E., and Farquhar, G. D. (1995). On the relationship between leaf anatomy and CO_2 diffusion through the mesophyll of hypostomatous leaves. *Plant, Cell and Environment*, 18(2):149–157.

Sánchez, D., Harvey, C., Grijalva, A., Medina, A., Vilchez, S., and Hernandez, B. (2005a). Diversidad, composicion y estructura de la vegetacion en un paisaje fragmentado de bosque seco en Rivas, Nicaragua. *Recursos Naturales y Ambiente*, 45:91–104.

Sánchez, D. M., Harvey, C., Grijalva, A., Medina, A., Vilchez, S., and Hernandez, B. (2005b). Diversidad, composicion, y estructura de la vegetacion en un agropaisaje ganadero en Matiguas, Nicaragua. *International Journal of Tropical Biology*, 53:387–414.

't Mannetje, L. and Haydock, K. P. (1963). The dry-weight rank method for the botanical analysis of pastures. *Journal of the British Grassland Society*, 18:268–275.

Tavares Corrêa Dias, A., van Ruijven, J., and Berendse, F. (2010). Plant species richness regulates soil respiration through changes in productivity. *Oecologia*, 163(3):805–813.

Thompson, K., Askew, A. P., Grime, J. P., Dunnett, N. P., and Willis, A. J. (2005). Biodiversity, ecosystem function and plant traits in mature and immature plant communities. *Functional Ecology*, 19:355–358.

Thompson, W. and Eldridge, D. (2005). Plant cover and composition in relation to density of *Callitris glaucophylla* (white cypress pine) along a rainfall gradient in eastern australia. *Australian Journal of Botany*, 53:545–554.

Tilman, D. (1988). *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, NJ.

Tilman, D. (1996). Biodiversity: population versus ecosystem stability. *Ecology*, 77(2):350–363.

Tilman, D. (2001). Functional diversity. In Levin, S. A., editor, *Encyclopedia of biodiversity*, volume 3, pages 109–120. Academic Press, San Diego, CA, USA.

Tilman, D., Cassman, K. G., Matson, P. A., Naylor, R., and Polasky, S. (2002). Agricultural sustainability and intensive production practices. *Nature*, 418:671–677.

Tilman, D. and Downing, J. A. (1994). Biodiversity and stability in grasslands. *Nature*, 367(6461):363–365.

Tilman, D., Duvick, D. N., Brush, S. B., Cook, R. J., Daily, G. C., Heal, G. M., Naeem, S., and Notter, D. R. (1999). Benefits of biodiversity. Technical report, Task force report 133. Council for Agricultural Science and Technology, Ames, IA.

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W. H., Simberloff, D., and Swackhamer, D. (2001). Forecasting agriculturally driven global environmental change. *Science*, 218:281–284.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., and Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science*, 277:1300–1302.

Tilman, D., Reich, P. B., and Knops, J. M. H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, 441(7093):629–632.

Tongway, D. and Ludwig, J. (1997). The nature of landscape dysfunction in rangelands. In Ludwig, J., Tongway, D., Freudenberger, D., Noble, J., and Hodgkinson, K., editors, *Landscape Ecology, Function and Management: Principles from Australia's Rangelands*, pages 49–61. CSIRO Publishing, Collingwood, Australia.

Trenbath, B. R. (1974). Biomass productivity of mixtures. *Advances in Agronomy*, 26:177–210.

Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., and Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecology Letters*, 8(8):857–874.

Turner, B. L. (2008). Resource partitioning for soil phosphorus: a hypothesis. *Journal of Ecology*, 96(4):1365–2745.

Tylianakis, J. M., Rand, T. A., Kahmen, A., Klein, A. M., Buchmann, N., Perner, J., and Tscharntke, T. (2008). Resource heterogeneity moderates the biodiversity-function relationship in real world ecosystems. *PLoS Biology*, 6(5):e122.

Van Arendonk, J. J. C. M. and Poorter, H. (1994). The chemical composition and anatomical structure of leaves of grass species differing in relative growth rate. *Plant, Cell and Environment*, 17(8):963–970.

van der Valk, A. G. (1981). Succession in wetlands: A Gleasonian approach. *Ecology*, 62(3):688–696.

Vandermeer, J., Lawrence, D., Symstad, A. J., and Hobbie, S. E. (2002). Effect of biodiversity on ecosystem functioning in managed ecosystems. In Loreau, M., Naeem, S., and Inchausti, P., editors, *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives*, pages 221–233. Oxford University Press, UK.

Vandermeer, J. and Perfecto, I. (2005). The future of farming and conservation. *Science*, 308:1257.

Vandermeer, J. and Perfecto, I. (2007). The agricultural matrix and a future paradigm for conservation. *Conservation Biology*, 21(1):274–277.

Vandermeer, J. H. (1989). *The Ecology of Intercropping*. Cambridge University Press, UK.

Varin, S., Cliquet, J., Personeni, E., Avice, J., and Lemauviel-Lavenant, S. (2010). How does sulphur availability modify N acquisition of white clover (*Trifolium repens* L.)? *J. Exp. Bot.*, 61(1):225–234.

Venables, W. N. and Ripley, B. D. (2002). *Modern Applied Statistics with S. 4th edition*. Springer, New York, USA.

Vickery, J. A., Bradbury, R. B., Henderson, I. G., Eaton, M. A., and Grice, P. V. (2004). The role of agri-environment schemes and farm management practices in reversing the decline of farmland birds in england. *Biological Conservation*, 119(1):19–39.

Vile, D., Garnier, E., Shipley, B., Laurent, G., Navas, M., Roumet, C., Lavorel, S., Díaz, S., Hodgson, J. G., Lloret, F., Midgley, G. F., Poorter, H., Rutherford, M. C., Wilson, P. J., and Wright, I. J. (2005). Specific leaf area and dry matter content estimate thickness in laminar leaves. *Annals of Botany*, 96(6):1129–1136.

Vile, D., Shipley, B., and Garnier, E. (2006). Ecosystem productivity can be predicted from potential relative growth rate and species abundance. *Ecology Letters*, 9(9):1061–1067.

Villéger, S., Mason, N. W. H., and Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89(8):2290–2301.

Violle, C., Navas, M., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., and Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, 116(5):882–892.

Vitousek, P. M., Mooney, H. A., Lubchenco, J., and Melillo, J. M. (1997). Human domination of earth's ecosystems. *Science*, 277:494–499.

Wackernagel, M., Schulz, N. B., Deumling, D., Linares, A. C., Jenkins, M., Kapos, V., Monfreda, C., Loh, J., Myers, N., Norgaard, R., and Randers, J. (2002). Tracking the ecological overshoot of the human economy. *Proceedings of the National Academy of Sciences (USA)*, 99(14):9266–9271.

Waggoner, P. E. (1995). How much land can ten billion people spare for nature? does technology make a difference? *Technology in Society*, 17:17–34.

Walker, B. (1995). Conserving biological diversity through ecosystem resilience. *Conservation Biology*, 9(4):747–752.

Walker, B., Holling, C. S., Carpenter, S. R., and Kinzig, A. (2004). Resilience, adaptability and transformability in social-ecological systems. *Ecology and Society*, 9(2):5.

Walker, B. H. (1992). Biodiversity and ecological redundancy. *Conservation Biology*, 6(1):18–23.

Walker, B. H. (2002). Ecological resilience in grazed rangelands: a generic case study. In Gunderson, L. H. and Pritchard, L., editors, *Resilience and the Behavior of Large-Scale Systems*, pages 183–193. Islands Press, Washington, DC, USA.

Walker, B. H., Kinzig, A., and Langdrige, J. (1999). Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems*, 2:95–113.

Walker, T. W., Adams, A. F. R., and Orchiston, H. D. (1955). The effects and interactions of sulphur, phosphorous and molybdenum on the growth and composition of clovers. *New Zealand Journal of Science and Technology*, A36:470–482.

Walker, T. W. and Gregg, P. E. H. (1975). The occurence of sulphur deficiency in New Zealand. In McLachlan, K. D., editor, *Sulphur in Australasian Agriculture*, pages 145–153. Sydney University Press.

Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä, H., der Putten, W. H. V., and Wall, D. H. (2004). Ecological linkages between aboveground and belowground biota. *Science*, 304:1629–1633.

Wardle, D. A., Naeem, S., and Li, S. (1998). A more reliable design for biodiversity study? *Nature*, 394:30.

Wardle, D. A. and Zackrisson, O. (2005). Effects of species and functional group loss on island ecosystem properties. *Nature*, 435(7043):806–810.

Wardle, P. (1991). *Vegetation of New Zealand*. Cambridge University Press, Cambridge, UK.

Warton, D. I., Wright, I. J., Falster, D. S., and Westoby, M. (2006). Bivariate line-fitting methods for allometry. *Biological Reviews*, 81(02):259–291.

Webb, C. J., Sykes, W. R., and Garnock-Jones, P. J. (1988). *Flora of New Zealand, Vol. IV: Naturalised Pteridophytes, Gymnosperms, Dicotyledons*. Botany Division, Department of Scientific and Industrial Research, Christchurch, New Zealand.

Webb, C. O., Ackerly, D. D., McPeek, M. A., and Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 33(1):475–505.

Webb, C. T., Hoeting, J. A., Ames, G. M., Pyne, M. I., and Poff, N. L. (2010). A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology Letters*, 13(3):267–283.

Weiher, E., Clarke, G. D. P., and Keddy, P. A. (1998). Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos*, 81(2):309–322.

Weiher, E. and Keddy, P. A. (1995). Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos*, 74:159–164.

Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, É., and Eriksson, O. (1999). Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science*, 10:609–620.

Welden, C. W. and Slauson, W. L. (1986). The intensity of competition versus its importance: an overlooked distinction and some implications. *Quarterly Review of Biology*, 61(1):23–44.

West, N. and Reese, G. (1991). Comparison of some methods for collecting and analyzing data on aboveground net production and diversity of herbaceous vegetation in a northern Utah subalpine context. *Vegetatio*, 96(2):145–163.

Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, 199(2):213–227.

Westoby, M. (1999). The LHS strategy in relation to grazing and fire. In Eldridge, D. and Freudenberger, D., editors, *Proceedings VI International Rangeland Congress*, pages 893–896. International Rangeland Congress Inc, Townsville, Australia.

Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A., and Wright, I. J. (2002). Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, 33:125–159.

Westoby, M., Walker, B., and Noy-Meir, I. (1989). Opportunistic management for rangelands not at equilibrium. *Journal of Range Management*, 42:266–274.

Winfree, R. and Kremen, C. (2009). Are ecosystem services stabilized by differences among species? a test using crop pollination. *Proceedings of the Royal Society B*, 276:229–237.

Witkowski, E. T. F. and Lamont, B. B. (1991). Leaf specific mass confounds leaf density and thickness. *Oecologia*, 88(4):486–493.

Wood, S. N. (2006). *Generalized Additive Models: An Introduction with R*. Chapman & Hall/CRC, Boca Raton, Florida, USA.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, É., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., Midgley, J. J., Navas, M. L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V. I., Roumet, C., Thomas, S., Tjoelker, M. G., Veneklaas, E. J., and Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428:821–827.

Wright, J. P., Naeem, S., Hector, A., Lehman, C., Reich, P. B., Schmid, B., and Tilman, D. (2006). Conventional functional classification schemes underestimate the relationship with ecosystem functioning. *Ecology Letters*, 9(2):111–120.

Yachi, S. and Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences (USA)*, 96:1463–1468.

Yamulki, S., Jarvis, S. C., and Owen, P. (1998). Nitrous oxide emissions from excreta applied in a simulated grazing pattern. *Soil Biology and Biochemistry*, 30:491–500.

Zsolnay, Á. (2003). Dissolved organic matter: artefacts, definitions, and functions. *Geoderma*, 113(3-4):187–209.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., and Smith, G. M. (2009). *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, USA.